The Beagle, Records of the Museums and Art Galleries of the Northern Territory, 2004 **20**: 87–166

A phylogenetic exploration of the catfish family Ariidae (Otophysi: Siluriformes)

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ABSTRACT

The phylogeny of the catfish family Ariidae is hypothesised based on examination of material from almost all regions of the family's circumglobal distribution yet concentrating on Sahul Shelf taxa. Morphological and osteological characters were investigated to determine which would usefully contribute to construction of a phylogeny for the family: 57 characters were selected and 35 rejected. Reasons for acceptance or rejection, and selection of outgroup, are provided. The cladograms resulting from phylogenetic analyses, and the distribution of character states within the family revealed the significant influence of homoplasy: acceptance of such is a necessary step however, to arriving at a reasonable phylogeny for this apparently straightforward yet incredibly diverse catfish family. Monophyly of the family was confirmed chiefly on the basis of thirteen characters. Twenty-three genera are recognised, including three new genera, *Amissidens*, *Cryptarius* and *Plicofollis*. The genera are diagnosed, their relationships discussed, and their species composition and geographical distribution are stated. The difficulty of assigning some taxa is revealed by placing them as *incertae sedae*; and the lack of access to some material is acknowledged as a hindrance to completion of a global revision.

KEYWORDS: Ariidae, family revision, fork-tailed catfishes, homoplasy, monophyly, revised classification, Sahul Shelf.

INTRODUCTION

Family characteristics. The Ariidae are catfishes belonging in the class Otophysi, subclass Siluriphysi, order Siluriformes (Fink and Fink 1996).

The Ariidae, or fork-tailed catfishes, are medium to large fishes having an elongate, robust body (Fig. 1). The head is conical to rounded or depressed. The mouth is terminal to inferior. The teeth are fine or stout, conical or wedge-shaped, sharp or blunt (granular). Jaw teeth are arranged into narrow or broad bands; palate teeth (when present) are grouped into large or small patches. Teeth may be present on the parasphenoid. The front and rear nostrils are usually close together on each side of the snout, the rear (posterior) one more or less covered by a flap of skin. Usually six barbels are present around the mouth: a pair of maxillary, a pair of mandibulary and a pair of mental (inner) barbels (reduced barbel complements are exhibited by *Osteogeneiosus* Bleeker, *Bagre* Cloquet and *Batrachocephalus* Bleeker (in part)).

The bony shield comprising part of the dorsal head surface is usually covered either by thin skin or exposed, but in some taxa it is concealed by thick skin and muscle. The head shield is smooth, rugose, striate or granular and in most taxa its posterior portion (the supraoccipital process) extends caudad to meet the predorsal (nuchal) plate. A dorsomedian groove or fontanel extending from the nostrils to the supraoccipital process is often apparent. The gill membranes are joined together and attached to the

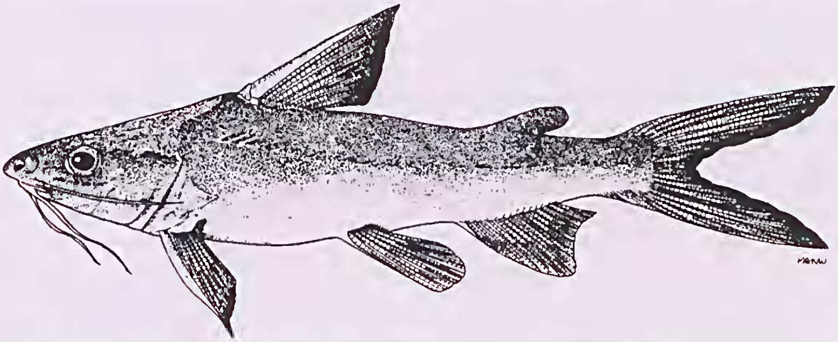

Fig. 1. *Ariopsis pectoralis*, a typical ariid catfish (200 mm SL). Illustration from Kailola (1999).

isthmus anteriorly, and the gill opening width varies from wide to restricted, wherein the gill openings do not extend ventrad to the pectoral fin base. There are 5–7 branchiostegals. The gill raker number on the anterior aspect of the first arch varies from 8 to 67. Rakers are always present along the posterior aspect of the third and fourth arches, sometimes on the first and second arches.

The body is naked with a well-developed lateral line commencing near the upper part of the gill opening and terminating on the tail base by turning dorsad or bifurcating over the caudal fin lobes. The dorsal fin, situated before the mid-length of the body, consists of a very short, broad spine (or spinelet or buckler), a long, usually serrated spine and seven branched rays. An adipose fin is always present and is situated above the spineless anal fin, which has 14–36 simple and branched rays. The pectoral fin is low-set and consists of a long, often serrated, spine and 7–13 branched rays. The pelvic (or ventral) fin has six branched rays and no spine; the shape of the inner ray is often modified in mature females. The caudal fin is deeply forked, with 15 (7+8) principal rays, and the outer ray of each lobe is unbranched.

The most significant internal features of the Ariidae are the firm-walled, free swim bladder, the elastic spring apparatus between the swim bladder and neurocranium, the extensive laminar of the fourth parapophyses which usually conceals the aortic canal, the complex vertebra comprising a single composite centrum formed by the fusion of the second to fourth vertebral centra, and the large auditory bulla containing an exceptionally large otolith.

Distribution. The Ariidae, or fork-tailed catfishes, are distributed almost circumtropically between about 35° N and 35° S. They are absent from Pacific waters between Australia and the island of New Guinea and the west coast of north, central and south America. Most ariids are confined to marine, coastal and estuarine habitats, but some are found (also) in freshwater rivers, streams and lakes; some marine taxa have been collected from depths to 150 m. Ariid catfishes are locally abundant in mangrove areas, large river estuaries and turbid waters.

Biology. Fork-tailed catfishes consume a variety of food items including detrital matter and a range of invertebrates, plants and fish. Although most species are generally omnivorous, some are specialised in dietary requirements. Larger individuals often feed solely on large crustacea, molluscs and teleosts.

The ariid catfishes are renowned for their method of reproduction (review: Rimmer and Merrick 1983). The females produce few, large (to 20 mm diameter) eggs which the male incubates in his buccal cavity after fertilisation until the young hatch and the yolk sac is resorbed.

Maximum attainable size ranges from 150 mm SL (*Nedystoma novaeguineae* (Weber)) to about 2 m SL (e.g., *Hemiarius stormii* (Bleeker)).

Classification. About 50 nominal genera have been described for the Ariidae (Eschmeyer 1990). The family comprises at least 350 nominal species, although valid species number about 125.

The great ichthyologists of the nineteenth century (Valenciennes 1840. 1840a; Müller and Troschel 1849; Bleeker 1858; and Eigenmann and Eigenmann 1890) grouped ariids from different world regions into several genera common to all regions. But later authors (e.g. Gill 1862; Bleeker 1862; Jordan and Evermann 1896–1900; Ogilby 1898; Weber 1913; Whitley 1940, 1941; Fowler 1944; Hubbs and Miller 1960) 'regionalised' the taxa such that new genera were erected largely on the basis of the geographical distribution of contained species. Consequently, the family is now classified into almost independent generic suites in Africa-Asia, Australia-New Guinea and the Americas.

There are inherent problems in interpretation of ariid characters due to the conservative phenotype of the family's taxa. Ariids exhibit an overall similarity in appearance which is emphasised by uniform colouration, habitat preference and biology. When considering the status of individuals in a catch of ariids – which overall are morphologically similar – most taxonomists 'solved' the problem of perceived differences in individual form by describing a new taxon. Early taxonomists were confused by the conservative ariid morphology and failed to recognise ontogenetic changes; their failure producing a plethora of nominal taxa. These earlier classifications extended beyond species to genera; and more genera came to include fewer species. For example, the 41 nominal species known in New Guinea and Australia alone prior to my study had been placed in 15 nominal genera: an average of 2.7 species per genus. Labile and adaptive features were often selected as being systematically important: for example, some nominal genera are based on characteristics such as lip thickness, mouth size, fin filament length, branchiostegal and barbel numbers and width of the branchial aperture.

This is the first attempt to appraise the status of nominal ariid genera on a world-wide basis. The status and composition of some genera were assessed in isolation by earlier workers: *Tachysurus* Lacépède (Jordan and Evermann 1896–1900; Chandy 1953; Jayaram 1982); *Felichthys* Swainson and *Ailurichthys* Baird and Girard (Jordan and Evermann 1896–1900); *Arius* Valenciennes, *Galeichthys* Valenciennes and *Ariodes* Müller and Troschel (Taylor 1986; Weber and de Beaufort 1913: *Arius*); and *Hemipimelodus* Bleeker (Désoutter 1977). Jayaram and Dhanze (1978) attempted a review of ariid genera but there are inadequacies in their investigation. Higuchi *et al.*'s

(1982) question regarding the validity of the inclusion of neotropical ariids in the genus *Netuma* Bleeker was, however, a firm beginning to the process of phylogenetic assessment of the family. Marceniuk and Ferraris Jr (2003) assessed the status of ariid genera and species of South and Central America.

My major study (Kailola 1990) concentrated on Australian and New Guinea (Sahul Shelf) ariids yet representatives of almost all nominal ariid genera were examined also. The study is based generally on a phylogenetic analysis of osteological and morphological characters of Australian and New Guinean representatives of the Ariidae. The osteological and morphological variation recorded among those ariids was compared with those of the apparently most widespread genus *Arius* Valenciennes (using the type of the genus, *A. arius* (Hamilton)) and of other nominal ariid genera (Table 1; Appendix A), and finally with homologous characters of other siluroids (Appendix B). The aims of the study are to:

1) identify characters useful in a phylogenetic analysis of ariids;

2) confirm the monophyly of the Ariidae; and

3) investigate the validity of nominal ariid genera and identify natural subgroups and phylogenetic relationships of ariid taxa, so forming a basis for future study on the family.

MATERIALS AND METHODS

Fish were collected from rivers and adjacent coastal waters of Australia, New Guinea, Asia, Africa and America. Most of the fishes collected are registered in international collections. However, some fresh specimens collected on commercial vessels, on field expeditions or in fish markets overseas could not be kept. Measurements and observations on them were recorded, however.

Skeletal preparations were made by clearing and staining representatives of all New Guinean and Australian ariid taxa except for *Tetranesodon conorhynchus* (Weber) (known only from the type), representatives of the type species of most ariid genera, and other siluroid species (Appendix B). Skeletal material of other species was also examined. The trypsin digestion methods of Taylor (1967) for single staining and Dingerkus and Uhler (1977) for double staining were largely employed; muscle tissue of some specimens was macerated in potassium hydroxide. Dry preparations of skulls and vertebral columns of several taxa were prepared by boiling the specimens before removing the soft tissue. Specimens were either single stained (in alizarin), double stained (in alizarin and alcian blue), or examined as dry skeletons. To assess intraspecific variation in the form and structure of bony tissue in adults and juveniles, several specimens representing a graded length range were processed whenever possible. Radiographs of specimens unavailable for processing (e.g., types) were also examined. Skeletal preparations and/or dry skeletons of extralimital (i.e., non Australo-New Guinea) ariid taxa and representatives of other catfish families were also studied.

In Appendix A the type species of nominal genera are identified, and asterisks indicate material examined more thoroughly. Institution acronyms are those of Leviton *et al.* (1985). Submitted to phylogenetic analysis were representatives of the type species of ariid genera not known to occur in Australia and New Guinea: *Hemiarius stormii*, *Bagre bagre*, *Ailurichthys marinus*, *Hexanematichthys sagor*, *Sciades emphysetus*, *Galeichthys feliceps*, *Guiritinga barbus*, *Arius arius*, *Ariopsis felis*, *Ariodes arenarius*, *Genidens genidens*, *Cathorops hypophthalmus*, *Hemipimelodus borneensis*, *Cephalocassis melanochir*, *Batrachocephalus mino*, *Osteogeneiosus militaris* and *Ketengus typus*. The character states of *Ancharius fuscus* were also analysed.

Synonymies were decided based on the material examined by me or by others on my behalf (Kailola 1990) or by study of definitive descriptions. Nominal species recorded in literature as synonyms of others are noted for some taxa: either identified specimens of these species have not been studied or the species' descriptions are not sufficient to determine their status.

Dates and authorities, unless checked by me, follow Eschmeyer (1998, 2003). Literature citations, unless seen by me, also follow Eschmeyer (1998, 2003).

Evolutionary relationships among the ariids were inferred using parsimony and the homology of characters was assessed. Ninety-two characters in almost all nominal ariid genera were identified, but 35 of those characters were not included in the phylogenetic analyses for reasons identified below. The states of the remaining 57 characters were scored; polarity was determined largely by comparison with an outgroup comprising other siluroids (Appendix B) and ostariophysans and primitive teleosts. My assessment was supplemented by ontogenetic transformation series and character trends. Many of the characters employed in the analysis are osteological but general morphological and functional features were also considered. Unfortunately, the character states of some complete features were not always treated as independent, and have been scored as one character (e.g., swim bladder shape and size, presence and shape of gill rakers, modifications of the laminar bone over the anterior vertebrae, fin spine shape and ornamentation).

The reasons why I considered particular characters to be unusable in the analyses are: (a) they are hard to qualify or quantify, either through assessment on suboptimal osteological preparations or through

Table 1. Nominal genera of the Ariidae, their type species and current taxonomic status (this paper). j.s. = junior synonym; o.s. = objective synonym; † = fossil (extinct) group; ms = manuscript name.

Nominal genus, author, date	Type species, author, date	Status
Aelurichthys Gill, 1863	*marinus* Mitchill, 1815	j.s. of *Bagre*
Ailurichthys Baird and Girard, 1854	*marinus* Mitchill, 1815	j.s. of *Bagre*
Amissidens new genus	*hainesi* Kailola, 2000	valid
Ancharius Steindachner, 1881	*fuscus* Steindachner, 1881	not Ariidae
Anemanotus Fowler, 1944	*panamensis* Gill, 1863	j.s. of *Bagre*
Ariodes Müller and Troschel, 1849	*arenarius* Müller and Troschel, 1849	j.s. of *Arius*
Ariopsis Gill, 1861	*milberti* Valenciennes, 1840 (= j.s. of *felis* Linnaeus, 1766)	valid
Arius Valenciennes, 1840	*arius* Hamilton, 1822	valid
Aspistor Jordan and Evermann, 1898	*luniscutis* Valenciennes, 1840	valid
Bagre Cloquet, 1816	*bagre* Linnaeus, 1766	valid
Batrachocephalus Bleeker, 1846	*ageneiosus* Bleeker, 1846 (= j.s. of *mino* Hamilton, 1822)	valid
Breviceps Swainson, 1838	*bagre* Bloch, 1794	name preoccupied by *Breviceps* Merrem; = *Bagre*
Brustiarius Herre, 1935	*nox* Herre, 1935	valid
Catastoma Valenciennes, 1840a	based on *nasutum* Kuhl and van Hasselt, ms	j.s. of *Netuma*
Cathorops Jordan and Gilbert, 1882	*hypophthalmus* Steindachner, 1875	valid
Cephalocassis Bleeker, 1857	*melanochir* Bleeker, 1852	valid
Cinetodus Ogilby, 1898	*froggatti* Ramsay and Ogilby, 1886	valid
Cochlefelis Whitley, 1941	*spatula* Ramsay and Ogilby, 1886	valid
Cryptarius new genus	*truncatus* Valenciennes, 1840a	valid
Doiichthys Weber, 1913	*novaeguineae* Weber, 1913	j.s. of *Nedystoma*
†*Eopeyeria* Whitley, 1947	*aegyptiacus* Peyer, 1928	replacement name for *Peyeria* (preoccupied)
Felichthys Swainson, 1839	*bagre* Bloch, 1794	replacement name for *Breviceps* Swainson; = *Bagre*
Galeichthys Valenciennes, 1840	*feliceps* Valenciennes, 1840	valid
Genidens Castelnau, 1855	*genidens* Valenciennes, 1840	uncertain
Glanide Agassiz in Spix and Agassiz, 1829		name not available
Glanis Agassiz in Spix and Agassiz, 1829	*bagre* Linnaeus, 1766	o.s. of *Bagre* Cloquet, 1816
Guiritinga Bleeker, 1858	*commersonii* Lacepede, 1803 (= j.s. of *barbus* Lacepede, 1803)	uncertain
Hemiarius Bleeker, 1862	*stormii* Bleeker, 1858	valid
Hemipimelodus Bleeker, 1857	*borneensis* Bleeker, 1851	j.s. of *Cephalocassis*
Hexanematichthys Bleeker, 1858	*sundaicus* Valenciennes, 1840 (= j.s. of *sagor* Hamilton, 1822)	valid
Ketengus Bleeker, 1847	*typus* Bleeker, 1847	valid
Leptarius Gill, 1863	*dowii* Gill, 1863	j.s. of *Sciades*
Mystus Gray, 1854	*carolinensis* Gray, 1854	not Ariidae
Nedystoma Ogilby, 1898	*dayi* Ramsay and Ogilby, 1886	valid
Nemapteryx Ogilby, 1908	*stirlingi* Ogilby, 1898 (= j.s. of *armiger* de Vis, 1884)	valid
Neoarius Castelnau, 1878	*curtisii* Castelnau, 1878 (= j.s. of *graeffei* Kner and Steindachner, 1866)	j.s. of *Guiritinga*
Netuma Bleeker, 1858	*netuma* Valenciennes, 1840 (= j.s. of *thalassinus* Ruppell, 1837)	valid
Notarius Gill, 1863	*grandicassis* Valenciennes, 1840	j.s. of *Hemiarius*
Osteogeneiosus Bleeker, 1846	*militaris* Valenciennes, 1840	valid
Pachyula Ogilby, 1898	*crassilabris* Ramsay and Ogilby, 1886	j.s. of *Cinetodus*
Paradiplomystes Bleeker, 1862	*coruscans* Lichtenstein, 1819	uncertain
Pararius Whitley, 1940	*proximus* Ogilby, 1898	j.s. of *Netuma*
†*Peyeria* Whitley, 1940	*aegyptiacus* Peyer, 1928	valid?
Pimelodus Bleeker, 1864	*bagre* Linnaeus, 1766	name preoccupied; = *Bagre*
Plicofollis new genus	*argyropleuron* Valenciennes, 1840a	valid
Potamarius Hubbs and Miller, 1960	*nelsoni* Evermann and Goldsborough, 1902	valid
Pseudarius Bleeker, 1862	*arius* Hamilton, 1822	j.s. of *Arius*
Sarcogenys Bleeker, 1858	based on *rostratus* Kuhl and van Hasselt, ms (= *thalassinus* Ruppell)	j.s. of *Netuma*
Sciadeichthys Bleeker, 1858	*emphysetus* Müller and Troschel, 1849	j.s. of *Sciades*
Sciadeops Fowler, 1944	*troschelii* Gill, 1863	j.s. of *Sciades*
Sciades Müller and Troschel, 1849	*emphysetus* Müller and Troschel, 1849	valid
Selenaspis Bleeker, 1858	*herzbergii* Bloch, 1794	j.s. of *Sciades*
Septobranchus Hardenberg, 1941	*johannae* Hardenberg, 1941	j.s. of *Cinetodus*
Stearopterus Minding, 1832	*bagre* Minding, 1832	may be same as *Bagre* (Eschmeyer, 1990)
Tachysurus Lacepede, 1803	*sinensis* Lacepede, 1803	nomen dubium
Tetranesodon Weber, 1913	*conorhynchus* Weber, 1913	j.s. of *Cinetodus*

perceived or suggested changes with ontogeny; (b) the character was obscured, damaged or altered by poor preservation; (c) assumptions about character states were required for different-sized individuals unavailable to me; (d) they present no phylogenetic information (for example, autapomorphies were generally excluded); (e) compared to their successful use in phylogenetic reconstruction in other catfish families, many characters in the Ariidae are either highly labile or very stable, exhibiting only intraspecific variation or parallel ontogenetic modifications (e.g., caudal skeleton form; shape of vertebral centra); (f) the characters are either meristic or morphometric: the problem with these characters is that there is no disjunction with the outgroup, making it difficult to determine polarity (Chernoff 1986); also, morphometric characters may be correlated with habitat and diet; and (g) ecologically adaptive characters are frequently homoplastic and correlated. In the ariids for example, mouth size, gut form, lip thickness, gill raker number, buccopharyngeal pad development, gill arch papillae, form, number and mobility of jaw teeth are all highly correlated with diet. Even so, some such characters were scored and included in the character matrix for analysis (Table 2).

The 35 rejected characters fall into three approximate groups (pp 113–119). Some of the equivocal and problematic characters could have contributed to a phylogenetic reconstruction. Of these, perhaps size or shape of skeletal characters (hyomandibular articular facet, fifth parapophyses, pelvic girdle, urohyal, parasphenoid alary processes, lateral ethmoid, third epibranchial uncinate process and supraoccipital), relative neurocranial ossification, form of the barbels and lateral line, eye position, and jaw tooth numbers, position, and mobility would be useful in phylogenetic analysis. Another character which perhaps should have been investigated is relative nostril shape. For example, the anterior nostril is 'tear'-shaped in *Cathorops*; and the posterior nostril is slit-like with crenulate margin in *Bagre*.

The homology of several bones is debated and confused in ostariophysan literature (compare Harrington 1955; Weitzmann 1962; Tilak 1963; Alexander 1965; Chardon 1968; Patterson 1975; Lundberg 1975; Gosline 1975; Arratia 1987). Clarification of bone homologies was beyond the scope of this study and so the nomenclature used here mainly follows that of Fink and Fink (1981) (who reviewed most of the ostariophysan skeleton) supplemented with observations and alternatives offered by Patterson (1975), Jollie (1986), Grande (1987), Schaefer (1987) and Vari (1989). Fink and Fink (1996) reviewed more recent literature relevant to interrelationships within major ostariophysan subgroups, particularly concentrating on the homology of bones (and some other structures).

Multistate character coding was performed for 78 taxa (including 24 outgroup taxa) using six states (0–5) with '?' for missing data. The matrix is presented as Table 2. The matrix was analysed using PAUP* version 4, beta 10 (Swofford 2002). Characters were unordered and of equal weight, a heuristic search and TBR (tree-bisection-reconnection) branch swapping was used, and the maximum number of trees was set at 500.

My initial (pre 1990) phylogenetic analyses were made using PAUP version 2.4.1 (Swofford 1986), which cannot handle more than 50 operational taxonomic units (Kailola 1990). Hence, several taxa featuring in the revised family structure I present below were not included in the original PAUP analysis (e.g., *Hemiarius sona*, *Aspistor* species, some *Sciades* species, *Cochlefelis burmanicus*) and I propose their status based on examination of whole and/or skeletal material and reliable literature. Of course this method is not ideal. However, it is the only one I now have available to complete a reasonable picture of the family: later researchers may care to prove or disprove my hypotheses.

Abbreviations used are: standard length = SL; head length = HL; cleared and stained = C&S; Br = branchiostegals; ESA = elastic spring apparatus; OTU = Operational Taxonomic Unit; HTU = Hypothetical Taxonomic Unit; RHS = right hand side; LHS = left hand side. A '†' sign before a name indicates that it is a fossil (extinct) group. The generic name standing alone refers to the type species of the genus. Vertebral counts are in the form of: anterior vertebral complex + thoracic vertebrae (open haemal arch) + haemal vertebrae (closed haemal arch with forked spine) + caudal vertebrae (closed haemal arch with unforked spine).

RESULTS AND DISCUSSION

Characters useful in a phylogenetic study of the Ariidae. Character recognition is a problem in the Ariidae and other catfish groups because of the overall lack of information on catfish biology and functional and descriptive morphology. Yet to enable meaningful application of phylogenetic methods to hypotheses of evolutionary relationships in the Ariidae, several intrinsic problems pertaining to character choice had to be addressed. Fortunately, problems in ascertaining character homology rarely arose in the Ariidae (fin spine form, neurocranial ossification and palatal dentition may be exceptions), although homologues in the outgroup (of other siluroids) were sometimes not so clear-cut. Another problem was that posed by incorporating correlated characters into a phylogenetic analysis, and ariids possess a number of correlated characters (e.g., those pertaining to the trophic and habitat requirements). Felsenstein (1982) pointed out that the effect of correlated characters can be to

Table 2. Character data matrix. Coded states are identified for 57 characters for Sahul Shelf ariids (*Ariopsis midgleyi* and *Ariopsis paucus* combined as one taxon), extralimital ariids and outgroup taxa.

Species	Characters																																																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57
Rita spp.	0	1	0	0	0	0	0	0	1	1	?	1	0	0	0	2	0	0	0	0	0	0	0	1	2	0	0	1	1	5	?	0	?	?	0	0	2	1	1	1	1	1	2	1	1	0	?	?	?	1	?	?	0	3	2	1	?
Pimelodus blochii	0	0	0	1	1	0	0	0	1	1	?	0	1	1	0	0	0	3	1	1	?	1	0	0	1	0	1	1	0	0	2	0	?	?	1	?	0	1	1	1	1	1	2	1	1	0	?	?	?	1	?	?	0	2	2	1	?
Rhamdia spp.	0	0	0	0	0	0	0	0	2	1	?	2	1	1	0	1	1	1	1	2	0	0	0	0	1	0	2	1	0	0	1	0	?	?	1	?	0	1	1	1	1	1	2	0	1	0	?	?	?	1	?	?	0	4	2	1	?
Anadoras grypus	0	2	2	0	0	0	0	1	1	1	?	?	0	0	1	3	0	2	?	3	0	2	0	1	2	0	?	0	2	4	1	0	?	?	1	?	0	1	1	?	1	?	?	1	1	0	?	?	?	1	?	?	1	4	?	0	?
Pterodoras sp.	0	2	2	0	0	0	0	1	1	1	?	?	?	0	1	3	0	2	?	3	0	2	0	1	2	?	?	0	0	0	1	0	?	?	1	?	0	1	1	?	1	?	?	1	1	0	?	?	?	1	?	?	1	4	0	0	?
Neosilurus sp.	0	0	0	0	0	0	0	0	0	1	?	1	0	3	0	1	0	1	1	3	0	2	0	1	2	0	2	1	?	4	0	0	?	1	0	0	4	1	1	1	1	1	2	3	5	2	0	?	?	1	?	?	0	4	2	1	?
Mystus sp.	0	0	0	0	0	0	0	0	0	1	?	2	?	3	?	0	?	1	1	?	?	0	?	?	1	1	1	1	1	0	1	0	?	?	0	0	2	1	1	1	1	1	?	0	1	2	0	?	?	0	0	0	0	4	1	1	?
Schilbe mystus	0	0	0	0	0	0	0	0	2	1	?	1	?	3	?	?	?	0	0	?	0	0	?	?	1	0	0	2	?	?	?	?	?	?	0	0	?	?	?	?	1	1	?	?	1	1	0	?	?	0	0	0	3	5	2	1	?
Pangasius hypophthalmus	0	0	0	0	?	1	0	?	0	1	?	0	?	?	0	0	?	3	0	?	0	?	0	0	?	1	0	?	2	3	?	?	?	?	0	0	?	1	0	?	?	1	0	0	1	?	?	?	?	?	?	?	0	5	?	1	?
Chrysichthys auratus	0	0	0	0	0	0	0	0	0	1	?	2	?	1	?	?	?	0	?	?	0	1	0	0	2	0	2	0	?	?	?	?	?	?	0	0	?	?	?	?	1	1	?	0	1	1	1	?	?	1	?	?	0	?	1	1	?
Bagrichthys macropterus	0	0	0	0	0	0	0	0	2	1	?	2	?	0	?	?	?	0	?	?	0	?	0	0	2	1	2	1	0	4	?	0	?	?	0	0	?	?	?	1	1	1	?	0	1	1	0	?	?	1	?	?	1	3	2	1	?
Synodontis macrostigma	0	0	2	0	0	0	0	1	0	1	?	1	?	0	?	?	?	0	?	?	0	1	?	?	2	1	2	0	0	0	?	?	?	?	1	?	?	?	?	1	1	0	?	?	1	0	?	?	?	1	?	?	1	?	2	?	?
Bagrus docmak	0	0	0	0	0	0	0	0	0	1	?	2	?	1	?	0	?	2	0	?	0	1	0	?	2	1	2	?	?	?	?	?	0	?	0	0	2	?	?	1	1	1	?	0	1	1	0	?	?	0	0	0	3	5	2	1	?
Ictalurus punctatus	0	0	0	0	0	0	0	0	1	1	?	2	?	1	?	?	?	0	0	?	0	?	0	?	2	1	1	1	?	?	?	?	?	1	0	0	?	?	?	1	1	1	?	2	1	2	0	?	?	1	?	?	0	3	1	1	?
Noturus flavus	0	0	0	0	0	0	0	0	1	1	?	0	?	3	?	?	?	0	?	?	0	1	0	1	2	1	0	2	?	?	?	?	?	1	0	0	?	?	?	1	1	1	?	2	5	1	0	?	?	1	?	?	0	2	2	1	?
Pylodictus olivaris	0	0	0	0	0	0	0	0	1	1	?	1	?	3	?	?	?	0	?	?	0	1	0	?	2	1	0	1	?	?	?	?	?	1	0	0	?	?	?	1	1	1	?	4	1	1	0	?	?	1	?	?	0	2	0	1	?
Parasilurus asotus	0	0	0	0	0	0	0	0	1	1	?	1	?	3	?	0	?	0	1	2	0	0	0	1	1	1	1	2	?	?	?	?	?	?	0	0	1	?	?	?	1	1	?	3	1	1	0	?	?	1	?	?	4	5	2	1	?
Ompok leiacanthus	0	0	0	0	0	?	?	0	?	1	?	?	?	3	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	3	?	0	?	?	1	?	?	1	1	?	?	1	2	1	1	?	?	?	?	0	0	0	4	5	?	1	?
Ompok miostoma	0	0	0	0	0	0	?	0	?	1	?	?	?	3	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	?	1	?	?	1	1	?	?	1	2	4	1	?	?	?	?	0	0	0	4	5	?	1	?
Silurichthys phaiosoma	0	0	0	0	0	?	?	0	?	1	?	?	?	3	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	3	?	0	?	?	1	?	?	1	1	?	?	1	2	1	1	?	?	?	?	1	?	?	4	?	?	1	?
Dianema spp.	0	0	0	?	?	?	?	0	?	1	?	?	?	2	0	3	?	?	?	?	?	?	?	?	?	?	?	2	1	1	?	0	?	1	1	?	?	1	1	?	?	?	0	0	2	?	?	?	?	1	?	?	2	0	?	0	?
Brochis splendens	0	0	0	?	?	?	?	0	?	1	?	?	?	2	1	3	?	?	?	?	?	?	?	?	?	?	?	2	1	1	?	0	?	1	1	?	?	1	1	?	?	?	0	0	2	?	?	?	?	1	?	?	3	0	?	0	?
Diplomystes chilensis	0	0	0	0	0	0	0	0	0	1	?	0	0	0	0	1	0	0	0	3	?	?	1	0	2	1	0	1	0	1	?	0	0	1	0	0	4	1	1	1	1	1	0	0	4	1	0	?	?	1	?	?	0	4	0	1	1
Hypostomus plecostomus	0	0	0	0	?	0	0	0	?	1	?	?	?	?	0	?	?	2	?	2	?	2	0	1	2	2	1	?	2	1	?	?	?	1	1	?	2	?	?	1	1	1	?	5	3	0	?	?	?	1	?	?	1	0	2	0	?
Hemiarius dioctes	1	2	2	2	1	1	1	1	2	0	0	1	1	1	0	0	0	3	1	0	0	0	0	0	0	3	2	1	1	0	2	1	2	0	0	0	0	1	1	1	1	1	2	0	0	1	0	0	0	0	0	0	1	3	0	1	1
Nemapteryx armiger	1	2	2	2	1	1	1	1	2	0	2	1	1	3	0	0	0	2	1	0	0	0	0	0	0	1	1	1	1	0	2	1	0	0	0	0	0	1	1	1	1	1	2	0	0	2	0	2	1	0	0	0	3	2	1	1	1
Netuma proximus	1	2	2	2	1	1	1	1	2	0	1	0	1	1	0	2	0	1	0	0	0	1	1	0	0	1	1	0	2	0	1	1	2	0	0	0	0	1	1	1	1	1	2	0	0	0	?	0	1	0	0	0	0	2	1	1	1
Hexanematichthys mastersi	1	2	2	2	1	1	1	1	2	0	1	0	1	1	0	1	0	1	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	?	0	1	0	0	0	1	2	0	1	1
Ariopsis latirostris	1	2	2	2	1	1	1	1	2	0	0	0	1	1	0	0	1	1	1	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0	0	1	0	1	1	0	0	0	0	2	1	1	1
Ariopsis leptaspis	1	2	2	2	1	1	1	1	2	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	1	1	1	1	2	0	0	0	?	0	1	0	0	0	0	2	0	1	1
Ariopsis midgleyi	1	2	2	2	1	1	1	1	2	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0	0	1	0	0	1	0	0	0	0	2	1	1	1
Nemapteryx augustus	1	2	2	2	1	1	1	1	2	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1	0	2	1	0	0	0	0	0	1	1	1	1	1	2	0	0	1	0	1	1	0	0	0	0	3	1	1	1
Ariopsis utarus	1	2	2	2	1	1	1	1	2	0	0	0	1	1	0	1	0	1	1	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0	0	1	0	0	1	0	0	0	0	2	1	1	1
Ariopsis graeffei	1	2	2	2	1	1	1	1	2	0	0	0	1	1	0	1	0	1	0	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	0	1	0	1	1	1	1	1	0	0	0	1	0	0	1	0	0	0	0	2	0	1	1
Ariopsis berneyi	1	2	2	2	1	1	1	1	2	0	0	0	1	1	0	2	1	1	0	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	0	1	0	1	1	1	1	1	0	0	0	1	0	0	1	0	0	0	0	2	1	1	1
Ariopsis pectoralis	1	2	2	2	1	1	1	1	2	0	0	0	1	1	0	1	0	1	0	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	1	?	0	1	1	1	1	1	0	0	0	1	0	0	1	0	0	0	2	2	1	1	1
Amissidens n.g. *hainesi*	1	2	2	2	1	1	1	1	2	0	1	0	1	3	0	3	2	0	0	1	0	1	0	0	0	3	0	1	2	0	0	0	0	0	1	?	0	1	1	1	1	1	0	0	0	2	0	2	2	0	0	1	3	2	1	1	1
Cinetodus froggatti	1	2	2	2	1	1	1	1	2	0	2	2	2	0	0	3	0	0	0	0	0	2	0	1	0	1	1	0	0	0	0	0	0	1	1	?	0	1	1	1	1	1	0	0	0	1	0	1	1	0	0	0	1	1	1	1	1
Cinetodus carinatus	1	2	2	2	1	1	1	1	2	0	2	2	2	0	0	3	0	0	0	0	0	2	0	1	0	2	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	0	0	0	1	0	1	1	0	0	0	1	2	1	1	1
Cinetodus crassilabris	1	2	2	2	1	1	1	1	2	0	2	2	1	0	0	3	0	0	0	0	0	2	0	1	0	2	0	1	0	0	0	1	0	1	1	?	0	1	1	1	1	1	0	0	0	2	0	2	1	1	?	?	0	2	2	1	1
Cochlefelis danielsi	1	2	2	2	1	1	1	1	2	0	0	0	1	1	0	0	0	2	1	0	0	2	0	0	0	1	1	0	0	0	2	1	0	?	0	0	0	1	1	1	1	1	2	0	0	2	0	0	1	0	0	0	0	2	1	1	1
Cochlefelis spatula	1	2	2	2	1	1	1	1	2	0	0	1	1	1	0	0	0	2	1	0	0	2	0	0	0	1	1	0	0	0	2	1	0	0	0	0	0	1	1	1	1	1	2	0	0	2	0	0	1	0	0	0	0	2	1	1	1
Nedystoma dayi	1	2	2	2	1	1	1	1	2	0	2	1	1	3	0	3	2	1	0	0	0	1	0	0	1	1	0	2	1	0	0	0	0	1	1	?	0	1	1	1	1	1	0	0	0	2	1	2	2	1	?	?	3	2	2	1	0
Nedystoma novaeguineae	1	2	2	2	1	1	1	1	2	0	2	1	0	3	1	0	0	3	2	2	0	0	0	0	1	1	1	2	1	0	2	0	0	1	1	?	3	1	1	1	1	1	0	0	0	2	1	2	2	0	0	0	2	2	2	1	0
Hemiarius insidiator	1	2	2	2	1	1	1	1	2	0	1	0	0	1	1	0	0	3	2	1	0	0	0	0	0	3	1	1	2	0	2	1	0	?	0	0	0	1	1	1	1	1	2	0	0	1	0	0	0	0	0	0	4	3	0	1	1
Netuma thalassinus	1	2	2	2	1	1	1	1	2	0	0	1	1	1	0	1	0	5	1	0	0	1	0	0	0	1	1	0	2	0	1	2	2	0	0	0	0	1	1	1	0	1	2	0	0	1	0	0	1	0	0	0	0	1	0	1	1
Netuma bilineatus	1	2	2	2	1	1	1	1	2	0	0	1	1	1	0	1	0	1	1	0	0	1	0	0	1	1	1	0	2	0	1	2	2	0	0	0	0	1	1	1	1	1	2	0	0	1	0	0	1	0	0	0	0	1	2	1	1
Plicofollis n.g. *argyropleuron*	1	2	2	2	1	1	1	1	2	0	1	0	1	1	0	2	1	0	0	1	1	1	0	0	0	3	1	0	2	0	0	2	3	0	1	?	0	1	1	0	0	1	1	0	0	1	0	1	2	0	1	0	0	2	1	1	1
Plicofollis n.g. *polystaphylodon*	1	2	2	2	1	1	1	1	2	0	1	0	1	1	0	2	1	2	0	1	1	1	1	0	0	3	2	0	1	0	0	2	1	?	1	?	0	1	1	1	0	1	1	0	0	1	0	1	2	0	1	0	0	2	0	1	1
Plicofollis n.g. *nella*	1	2	2	2	1	1	1	1	2	0	0	0	1	1	0	2	1	2	0	1	1	1	1	0	0	3	2	0	1	0	0	2	1	?	1	?	0	1	1	1	0	1	1	0	0	1	0	1	2	0	1	0	0	2	0	1	1
Aspistor hardenbergi	1	2	2	2	1	1	1	1	2	0	1	1	1	1	0	1	0	1	0	0	0	1	1	0	0	1	1	1	0	0	1	1	0	?	0	0	0	1	1	1	1	1	2	0	0	1	0	1	1	0	0	0	1	2	0	1	1
Brustiarius nox	1	2	2	2	1	1	1	1	2	0	1	0	1	3	0	0	2	1	1	0	0	1	0	0	1	2	2	1	2	0	1	1	0	0	0	1	0	1	0	1	1	1	2	0	0	1	0	1	1	0	0	0	3	2	2	1	1
Brustiarius solidus	1	2	2	2	1	1	1	1	2	0	1	0	1	1	0	0	0	2	1	0	0	1	0	0	1	2	2	1	2	0	1	1	0	0	0	1	0	1	0	1	1	1	2	0	0	1	0	1	1	0	0	2	0	2	1	1	1
Ariopsis coatesi	1	2	2	2	1	1	1	1	2	0	1	1	1	1	0	1	0	1	1	0	0	1	0	0	0	1	1	0	1	0	1	1	0	?	1	?	0	1	1	1	1	1	1	0	0	2	0	2	1	0	0	0	0	2	1	1	1
Ariopsis velutinus	1	2	2	2	1	1	1	1	2	0	1	0	1	1	0	1	1	1	1	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	1	?	0	1	1	1	1	1	1	0	0	2	0	1	1	1	?	?	0	2	1	1	1
Ariopsis robertsi	1	2	2	2	1	1	1	1	2	0	1	0	?	1	0	1	1	1	?	?	0	?	0	0	0	?	?	0	1	0	1	1	?	0	1	?	0	1	1	1	1	1	1	0	0	2	1	2	1	1	?	?	0	2	1	1	1
cf. *Arius macrorhynchus*	1	2	2	2	1	1	1	1	2	0	1	0	1	1	0	2	0	4	2	1	0	1	0	0	0	2	2	0	2	0	0	1	0	0	1	?	0	1	1	1	1	1	1	0	0	2	0	0	2	1	?	?	3	2	1	1	1
Cinetodus conorhynchus	1	2	2	2	1	1	1	1	2	0	?	1	?	0	0	3	0	0	0	?	?	?	?	?	0	?	?	1	0	0	0	1	?	?	1	?	0	1	1	1	1	1	0	0	0	?	?	?	?	1	?	?	1	2	2	1	1
Arius arius	1	2	2	2	1	1	1	1	2	0	1	0	1	1	0	1	1	0	0	0	0	1	0	0	1	2	1	0	1	0	1	1	0	0	0	0	0	1	1	1	1	1	0	0	0	1	0	1	1	0	0	0	0	2	1	1	1
Galeichthys feliceps	1	2	1	1	0	1	1	1	2	0	0	1	1	2	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	1	0	0	0	1	1	1	1	1	0	0	0	1	1	1	0	0	0	0	3	2	1	1	1
Ancharius brevibarbis	?	2	?	0	1	0	0	?	0	1	?	?	?	1	0	3	0	0	2	1	0	2	?	?	?	1	2	1	0	0	1	1	?	?	1	?	?	1	1	1	1	1	2	0	0	0	?	?	?	1	?	?	2	?	1	1	1
Ariopsis felis	1	2	2	2	1	1	1	1	2	0	1	0	?	1	0	2	1	1	0	0	0	1	0	0	1	2	1	0	1	0	1	1	?	0	0	0	0	1	1	1	1	1	2	0	0	1	0	1	1	0	0	0	0	2	1	1	1
Batrachocephalus mino	1	2	2	2	1	1	1	1	2	0	1	0	1	1	0	2	0	3	2	2	0	1	0	0	2	3	0	0	1	2	?	2	0	?	1	?	0	1	1	1	1	1	0	0	0	0	?	1	0	0	0	0	1	1	1	1	1
Osteogeneiosus militaris	1	2	2	2	1	1	1	1	2	0	1	0	1	3	0	0	0	3	1	2	0	1	0	0	1	3	0	1	1	1	?	2	2	1	1	?	0	1	1	1	1	1	0	0	0	1	0	2	1	0	0	0	3	2	1	1	1
Genidens genidens	1	2	2	2	1	1	1	1	2	0	0	0	1	3	0	2	0	0	0	0	0	1	0	0	1	2	1	0	0	0	1	0	?	?	1	?	0	1	1	1	1	1	1	0	0	1	0	1	1	0	0	0	0	2	1	1	1
Bagre bagre	1	2	2	2	1	1	1	1	2	0	0	2	1	3	0	1	?	3	2	2	0	0	1	0	0	2	0	2	2	3	?	2	?	?	0	0	?	1	1	1	1	1	2	0	0	0	?	0	1	0	0	0	3	2	2	1	1
Hexanematichthys sagor	1	2	2	2	1	1	1	1	2	0	0	0	1	1	0	1	0	1	1	0	0	1	0	0	2	1	1	0	1	0	1	1	0	0	0	0	0	0	1	1	1	0	2	0	0	0	?	0	1	0	0	0	1	2	0	1	1
Cephalocassis borneensis	1	2	2	2	1	1	1	1	2	0	2	1	1	3	1	3	2	0	0	0	0	1	0	0	2	2	1	1	0	0	0	2	0	0	1	?	1	1	1	1	1	1	0	0	0	2	1	2	2	1	?	?	3	1	2	1	?
Cephalocassis melanochir	1	2	2	2	1	1	1	1	2	0	2	1	1	3	1	3	2	0	0	0	0	0	0	0	1	2	2	1	0	0	0	1	?	?	1	?	1	1	1	1	1	1	2	0	0	2	1	2	2	0	0	0	0	2	1	1	1
Cathorops hypophthalmus	1	2	2	2	1	1	1	1	2	0	2	2	1	3	1	3	1	2	2	0	0	0	1	1	2	2	1	1	2	0	1	1	?	1	1	?	0	1	1	1	1	1	0	0	0	0	?	2	3	0	0	0	0	2	2	1	?
Bagre marinus	1	2	2	2	1	1	1	1	2	0	0	1	1	3	0	?	?	2	1	1	0	?	1	0	1	1	0	1	1	3	?	?	0	0	0	0	2	1	1	1	1	1	2	0	0	1	1	0	1	0	0	0	3	2	1	1	1
Sciades emphysetus	1	2	2	2	1	1	1	1	2	0	0	?	?	1	0	1	0	1	0	0	0	?	1	0	0	?	?	0	1	0	1	1	0	1	0	0	?	1	1	1	1	0	2	0	0	0	?	1	1	0	0	0	1	?	0	1	?
Guiritinga barbus	1	2	2	2	1	1	1	1	2	0	0	0	1	1	0	2	0	1	0	0	0	1	?	0	2	2	1	0	1	0	1	1	?	?	0	0	0	1	1	1	1	1	0	0	0	0	?	0	1	0	0	0	0	2	1	1	1
Guiritinga planifrons	1	2	2	2	1	1	1	1	2	0	0	0	1	1	0	1	0	1	1	0	0	1	?	0	1	1	1	0	1	0	1	1	?	?	0	0	0	1	1	1	1	1	0	0	0	1	?	0	0	0	0	0	0	2	1	1	1
Ariodes arenarius	1	2	2	2	1	1	1	1	2	0	1	?	?	1	0	1	1	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	0	0	?	?	?	1	1	1	1	1	0	0	0	?	?	?	?	0	0	0	0	2	1	1	1
Ketengus typus	1	2	2	2	1	0	1	1	2	0	1	0	1	3	0	3	0	2	1	2	0	2	0	0	1	3	0	1	1	0	1	2	0	?	1	?	?	1	1	1	1	1	2	0	0	0	?	?	1	1	?	?	0	2	2	1	1
Hemiarius stormii	1	2	2	2	1	1	1	1	2	0	1	1	1	1	0	0	0	3	0	0	0	0	0	0	0	2	1	1	0	0	2	1	2	?	0	0	0	1	1	1	1	1	2	0	0	2	1	2	0	0	0	0	1	2	1	1	1
Cryptarius n.g. *truncatus*	1	2	2	2	1	1	1	1	2	0	1	0	2	1	0	3	0	2	0	0	1	2	1	0	1	1	0	1	1	0	0	2	2	?	1	?	0	1	1	1	1	1	0	0	0	1	0	1	0	0	0	0	1	2	1	1	1

produce quite different interpretations in tree reconstruction. Detecting these characters all too frequently depends on functional analysis of the study group, a task that has been largely ignored in the Siluriformes. Furthermore, Maddison *et al.* (1984) drew attention to the problem that characters that are labile in an outgroup may be equally labile in the ingroup and so cannot confidently be used to resolve the ingroup. Hence, recognition of reliable, independent, non-osteological characters proved to be a particularly vexing problem. Some characters I analysed were not used in phylogenetic reconstructions using PAUP.

Ninety-two characters were assessed. The first 57 were used for phylogenetic analysis although some of them are correlated or ecologically adaptive (e.g., extent of the gill openings, relative development of buccopharyngeal tissue, swim bladder shape, and presence of rakers along the back of the gill arches), sixteen are relevant to an assessment of the whole family (see below), and others are possibly autapomorphic (e.g., shape of particular bones, such as lachrimal and mesethmoid). Even so, those adaptive characters included in the phylogenetic analysis are obvious and characteristic taxonomic features.

Thirty-five characters investigated but not used in the analyses are listed after the list of characters used, albeit some of them potentially could lend support to identified relationships. The basis for their rejection in the analyses was my attempt to determine homoplasies beforehand, through the process of character weighting during earlier analyses (Kailola 1990). Following Arnold (1981), those characters that are more internally consistent, extensive and complete were weighted more heavily than were characters that show great intraspecific variability, are affected by ecological shifts, are difficult to score, are present in distantly-related taxa, and/or appear to be highly labile in both outgroup and ingroup.

Monophyly of the Ariidae. The monophyly of the Ariidae is established by the combination of the following characters: the habit of oral incubation (Character 1); the absence of a mesocoracoid (a derived character state shared with other taxa (Doradidae, Mochokidae)); the frontal and mesethmoid meeting at a minimum of two sites (except in *Ketengus*: one site); possession of strong pelvic musculature, a naked body and large otolith; and formation of an aortic tunnel, homologous elastic spring apparatus (ESA) and extended epioccipital and absence of a supraneural (except in *Galeichthys*, these four characters). Even so, some of these character states are frequently present in the Pimelodidae.

Another four characters (synapomorphies) are presumed to support monophyly. These characters were not included in the analysis. They are listed below.

Epidermal viscous mucus secretions. These secretions are unaffected by thiols, have heat-labile protease (sensitive red blood cell lytic factor) and a protein factor that accelerates clotting of plasma. Such features are not present in the secretions of other catfishes (Di Conza 1970; Al-Hassan *et al.* 1985). The mucus from *Arius* is a unique secretion of physiological importance and appears to be a novel anti-predatory adaptation (Al-Hassan *et al.* 1985). This secretion may be a modified fright substance (Pfeiffer 1977; Fink and Fink 1981).

Maximal consolidation of the anterior vertebrae. Up to three and four subsequent vertebrae are firmly articulated with the complex vertebra in ariids, on average more than in any other siluroid family (Bhimachar 1933; Howes 1983; Tilak 1965; Roberts 1973; pers. obs.). The number of rigidly-united vertebrae is largely associated with the length of the specimen, the investing (laminar) bone gradually extending backward with age (and see Regan 1911). Although Taylor (1986) used the extent of laminar bone to partly diagnose *Galeichthys*, in general this is not a sound character.

Exceptionally firm articulation of the vertebral column (and therefore the trunk) with the skull. (Bhimachar 1933; Tilak 1965). In addition to the normal attachment of the first vertebra centrum with the skull, the ariids exhibit firm unification at the subvertebral cone, the epioccipital flange and the transverse process of the fourth vertebra, the neural process of the fourth vertebra with the supraoccipital and the exoccipital above the foramen magnum (Bhimachar 1933). Mahajan (1966) concluded that a solid connection of the vertebral column with the skull led to a more efficient functioning of the sound-producing apparatus in the Sisoridae; an apomorphy which may well hold true for the Ariidae.

Precocial larvae. Among catfishes, only the Ariidae and the Loricariidae produce such larvae, with the large young resembling the adult in every aspect of external morphology yet retaining a large yolk sac. Such a developmental feature is a significant specialisation over many catfish families whose larvae are atricial (Fuiman 1984).

Monophyly is also suggested by fin ray number and genetic studies. In all taxa the dorsal fin consists of a spinelet, a spine and seven branched rays; the caudal of 15 (7+8) branched and two unbranched principal rays; and the pelvic fin of six branched rays. Studies on the DNA complement (LeGrande 1980) and karyotype of several ariid taxa (Fitzsimmons *et al.* 1988) have revealed features suggesting monophyletic grouping: e.g., high DNA complement per cell, chromosome number and arm length.

The status of *Ancharius* as an ariid merits attention. The phylogenetic analysis performed here casts doubt on the position of *Ancharius* within the family Ariidae (Fig 15). This taxon possesses an open aortic canal, low auditory bulla and reduced otolith, an unproduced epioccipital, short and fine nasal barbels (fringed in *A. brevibarbis*), a supraneural before the nuchal plate and an expanded Mullerian ramus. *Ancharius* has a close affinity with the Mochokidae and it is prudent to remove it from the Ariidae. Indeed, Glaw and Vences (1994; in Ferraris Jr and de Pinna 1999) listed *Ancharius* as the type genus of the family Anchariidae.

Character states and their assigned (inferred) polarities. In view of the poor definition of ariid features in systematic literature and the often flimsy bases for generic nomination, clear character descriptions and evaluations are needed. A real contribution to a future, broader assessment of the family's relationships in the suborder Siluriformes can be made by redescribing homologous and uniquely derived features of ariid morphology along the lines established by recent studies of other siluroids. Furthermore, comparison of homologous characters and ecological adaptations with those of other siluroids provides additional evidence for the role of environment in speciation.

1. *Oral incubation – low fecundity.* Within the Siluriformes, the habit of orally incubating eggs and young is unique to the Ariidae and some Bagridae (Ochi *et al.* 2002). Oral incubation in the Ariidae is well described for many genera (Rimmer and Merrick 1983; Rimmer 1985) and the presence of few, large-sized ova in mature females clearly indicates the phenomenon of parental care (Oppenheimer 1970). Ochi *et al.* (2002) reported that eggs brooded in the mouth of male *Lophiobagrus aquilas* were adhesive and attached to each other in a mass, while the eggs brooded by male Ariidae and both parents in two species of the bagrid genus *Phyllonemus* Boulenger are individually separated. For the Ariidae, this statement is not correct, as is the authors' supposition that eggs clumped together are liable to heavier predation at spawning, and that males incubate egg masses because they can more quickly take them into their mouth than can females. As Dmitrenko (1974) has demonstrated, and many others (including self) have witnessed, adult ariids are able to scoop up the single bundle of adhesive eggs in one movement, and the eggs being clumped together is an advantage as this prevents individual eggs from being lost in the water currents, or buried in the silt or debris of the substrate. Once in the male's mouth, enzymes break up the binding mucus, so enabling the male to turn the eggs around in his mouth for oxygenation and even development (refer Rimmer and Merrick 1983). Furthermore, the reason only male ariids incubate is not that they are quicker at picking up the egg mass but because they have a sufficient fat store to tide them over the required 4–6 week incubation period (see also Rimmer (1985) and Rimmer and Merrick (1983)). Females do not have the body condition for such a long incubation period, their energies having been used up in growing the large eggs.

Parental care not involving oral incubation is practised in some other catfish families, such as the Loricariidae, Aspredinidae and Ictaluridae; also Bagridae (Breder 1935).

State 0 = oral incubation not practised; 1 = oral incubation practised.

2. *Mesocoracoid.* The mesocoracoid is absent from the pectoral girdle of the Ariidae, Bunocephalinae (Aspredinidae) and Doradidae (Regan 1911; Tilak 1965; Greenwood *et al.* 1966). In *Rita* (Bagridae) this bone is represented by a short hook-like process (Bailey and Stewart 1984; pers. obs.). Loss of the mesocoracoid is a derived feature as it is present in all other siluroids, including the †Hypsidoridae and Diplomystidae.

State 0 = mesocoracoid present; 1 = mesocoracoid incomplete; 2 = mesocoracoid absent.

3. *Epioccipital extension.* In the Ariidae, the epioccipital is produced posteriorly into a long process which articulates more or less with the dorsal aspect of the superficial laminar bone of the anterior fused vertebrae (Fig. 2); albeit in *Galeichthys* the bone is only slightly produced and does not contact the laminar bone of the anterior fused vertebrae. The only other siluroids sharing the derived state of the epioccipital extension are the Auchenipteridae and the doradid genus *Pterodoras* (Regan 1911; Gosline 1975; Curran 1989), although the form of the bone posteriorly in these taxa is not homologous with that in the ariids.

4. *Aortic tunnel.* In almost all ariids, the superficial bone of the complex and other anterior vertebrae spreads over the aortic canal, so forming a tunnel. In *Ancharius*, the aortic canal remains open; in *Galeichthys* the tunnel is partial or absent. In the few small ariid specimens examined (less than 50 mm SL; three species) the canal is open. Concealment of the canal in adults – often by a thick sheet of bone – appears to be derived within the catfishes. Only in *Pimelodus* (outgroup material) and eleven other pimelodid genera (Howes 1983) is the canal largely concealed.

State 0 = open aortic canal at all stadia; 1 = aortic canal partially closed in adult; 2 = aortic canal completely covered to form a tunnel in all stadia beyond mouth juveniles.

5. *Supraoccipital – nuchal plate articulation.* The primitive condition in catfishes is the presence of one or more supraneurals between the nuchal plate and the supraoccipital (Arratia 1987; Grande 1987). The supraneural is prominent in bagrids, many pimelodids (J. Lundberg pers. comm.), doradids and *Synodontis* (outgroup material). In all ariids except *Galeichthys*, the supraneural is not exposed in the dorsal surface and the supraoccipital rigidly articulates with the nuchal

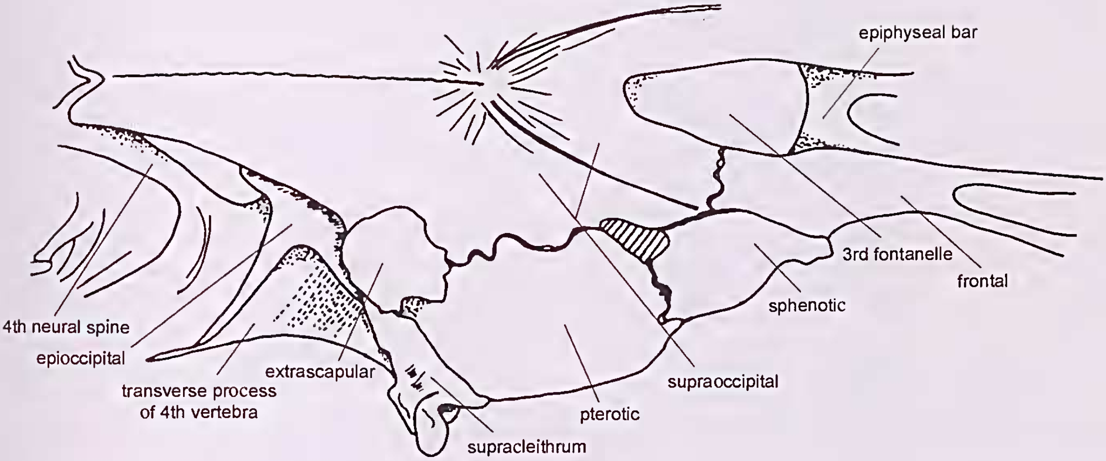

Fig. 2. Posterolateral view of *Cephalocassis borneensis* neurocranium, showing epioccipital extending over laminar bone of anterior vertebrae (123 mm SL).

plate. Only *Pimelodus* in the outgroup material shares this derived condition.

State 0 = supraoccipital-nuchal plate connection interrupted by a supraneural; 1 = supraoccipital articulates directly with nuchal plate.

6. *Lateral ethmoid – frontal articulation.* In the vast majority of catfishes the lateral ethmoid articulates with the frontal by one facet. The Ariidae and Pangasiidae exhibit a derived condition within the Siluriformes in which there are two facets: articulations of two processes from each bone. In the Ariidae the median arm of the frontal articulates with the lateral ethmoid and mesethmoid, and the lateral arm of the frontal articulates with the lateral ethmoid wing (Fig. 3). The sturdiness and length of the lateral arm varies within the family, from thin and long to very stout and short. There is some intrafamilial variation however: *Ketengus* possesses only one frontal-lateral ethmoid connection; and in *Bagre* a long process from the mesethmoid makes a third posterior connection with the frontal.

State 0 = single lateral ethmoid–frontal articulation; 1 = at least dual articulation.

7. *Otolith size and auditory bulla.* The auditory bulla and lapillus otolith are exceptionally large in ariids (not so large in *Galeichthys*). The bulla is formed by swelling of part of the prootic, pterotic and exoccipital. Characiforms also have a pronounced bulla (Fink and Fink 1981). All other catfishes have a much reduced otolith and bulla when compared with the ariids (e.g., Regan 1911; Chardon 1968; pers. obs.). *Ancharius* has a reduced otolith and shallow bulla.

State 0 = moderate to small otolith and bulla; 1 = enlarged otolith and bulla.

8. *Elastic spring apparatus (ESA).* All ariids except *Galeichthys* (Kulongowski 2001) possess a set of muscles connecting the anterolateral arm of the Mullerian ramus (see below) to the neurocranium and anterior vertebrae. This system forms an ESA (or mechanism) which functions to produce a gas resonance in the swim bladder. Tavolga (1962) presented an excellent description and functional analysis of the ariid ESA; Alexander (1965), Howes (1983) and Fink and Fink (1996) suggested possible homology and phylogenetic implications.

An ESA is found in several catfish families (Regan 1911; Howes 1985; Curran 1989): Doradidae (then including the Ageneiosidae and Auchenipteridae), Mochokidae, Malapteruridae and Pangasiidae, as well as the Ariidae. Royero (1988) believed that the ESA is structurally homologous in all of these families except in the Pangasiidae and Malapteruridae (and see comment in Curran 1989).

State 0 = ESA absent or independently derived; 1 = ESA present, homologous structure.

9. *The Mullerian ramus.* The Mullerian ramus is the anterior limb of the fourth vertebral parapophysis (or transverse process). In the Ariidae (except *Galeichthys*) it is free from the supracleithrum and curves ventrad to contact the tunica externa of the swim bladder (Fig. 4).

A relatively primitive, smoothly curved configuration of the transverse process lamina is present in the Ariidae, the Diplomystidae, Ictaluridae, †Hypsidoridae (Grande 1987), some Bagridae and Pimelodidae (Lundberg and McDade 1986). However, variation occurs in these families. For example, in *Hemiarius insidiator*, the ramus is abbreviated and angular, and it is comparatively long in *Hemiarius dioctes*, *Amissidens* n. gen. *hainesi*, *Cinetodus froggatti*, *C. carinatus*, *C. crassilabris*, *Ariopsis midgleyi*, *Nemapteryx augustus* and *Nedystoma*

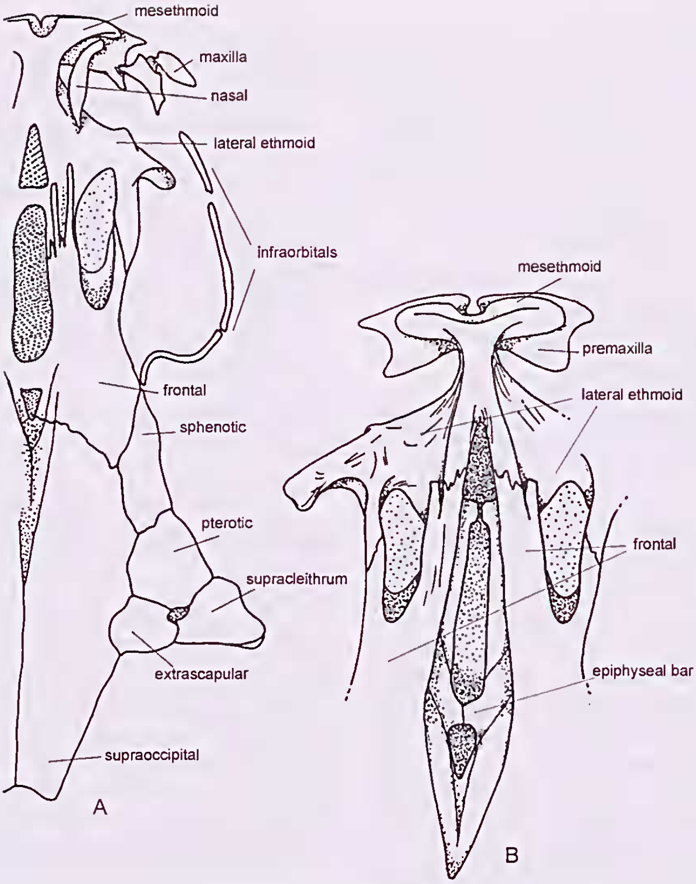

Fig. 3. *Arius arius*. **A**, Dorsal view of neurocranium and infraorbitals (190 mm SL); **B**, enlarged view with nasal bone omitted (112 mm SL).

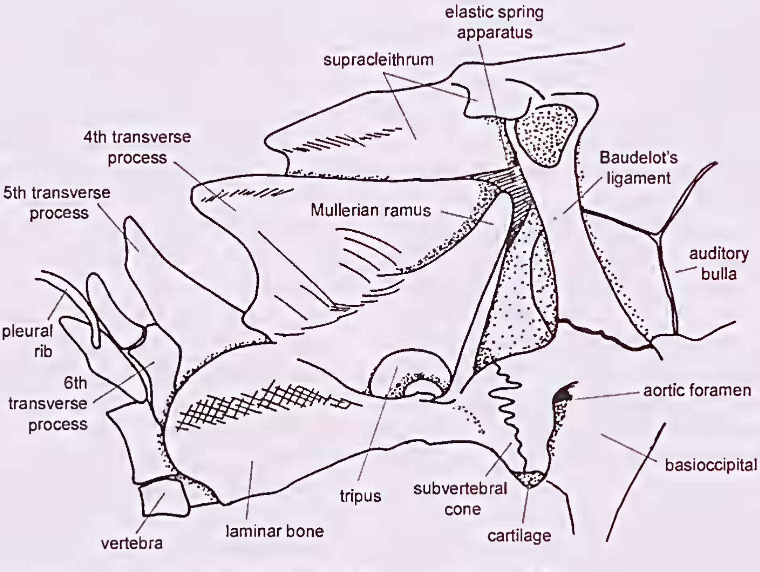

Fig. 4. Ventrolateral view of posterior part of right side of skull of *Arius arius* (112 mm SL).

dayi. In other siluroids (such as *Ancharius* and *Synodontis* (Mochokidae), the ramus is much expanded and disc-like.

State 0 = ramus tip expanded; 1 = tip truncate to moderately attenuated, slightly curved; 2 = tip very attenuated, well curved.

10. *Subvertebral cone*. The laminar bone over the first and complex vertebrae is well elevated anteromedially in *Schilbe* and the plotosid *Neosilurus*, and low in most other catfishes. Only the Ariidae have a sheet of bone concealing the fusion of the basioccipital and the anterior vertebral complex (Fig. 5). The first vertebra is completely (or almost) concealed and the laminar sheet forms a 'subvertebral cone' at the fusion site, a condition I consider derived.

State 0 = subvertebral cone present; 1 = cone absent.

11. *Subvertebral cone shape and size*. A strong suture unites the basioccipital and the laminar bone to form the subvertebral cone, which projects in varying degrees. The tip may be bifurcate and is often cartilage-covered. In the genera *Galeichthys*, *Ancharius* and *Bagre* the subvertebral cone is low, with a deep median excavation (aortic tunnel incomplete) in the first two taxa. In taxa having a low cone, the basal aortic foramen opens downward. With increasing length and expansion of the cone, the foramen comes first to open obliquely, then to open forward from a position in the angle at the anterior base of the cone.

Whereas the subvertebral cone is flat in some taxa (e.g., *Bagre bagre*), in most it is moderately elevated. The cone attains its most extreme development in *Cathorops*, *Cephalocassis*, *Nemapteryx armiger*, *Cinetodus*, *Nedystoma dayi* and *N. novaeguineae*. I consider this high, stout cone as the apomorphic condition.

State 0 = low subvertebral cone; 1 = moderately elevated cone; 2 = well elevated, strong cone.

12. *Fourth neural spine – epioccipital flange*. The transverse process of the complex centrum is broadly expanded in a horizontal plane and it and the fused neural arches form a roof over the neural canal (Fig. 6). Tilak (1965) placed considerable importance on the disposition and height of the ridges or laminae on the dorsal surface of the so-formed 'pars sustentaculum'. The flanges of the fourth neural arch may function as a strut in support of the dorsal fin-skull articulation.

There are four general groups of laminae form:

1) In *Arius arius* the lateral ridges and the forward ridges (or laminae) of the fourth neural spines are low and concave. However, in some taxa the lateral ridge is high, extending half-way up the neural spine, and in several other taxa the lateral ridge is moderately elevated. *Cathorops* has an exceptionally high transverse lamina.

2) The forward ridge from the fourth neural spine to the third is moderately elevated to very high in some ariids.

3) Whereas the posteromedian flange of the epioccipital attaches to the dorsal surface of the complex centrum or its lamina in most ariids, in some taxa it abuts the lateral ridge or lamina of the fourth neural spine and may be very well elevated.

4) Several taxa (e.g., *Cinetodus froggatti*, *Galeichthys*, *Aspistor kessleri* and *Bagre marinus*) have

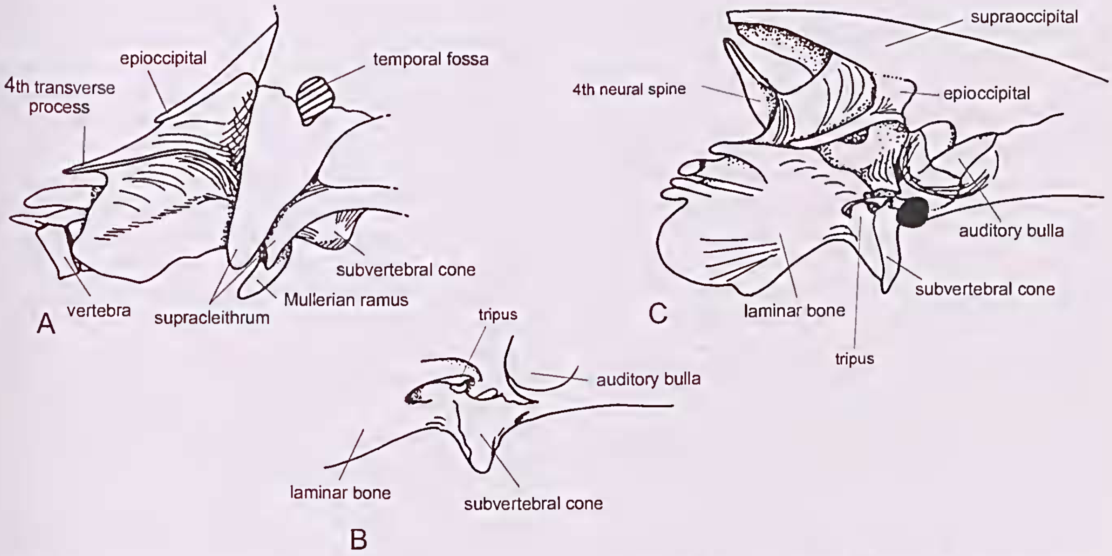

Fig. 5. Relative size of subvertebral cone in **A**, *Ariopsis coatesi*, 237 mm SL; **B**, *Ariopsis robertsi*, 108 mm SL; and **C**, *Cinetodus crassilabris*, 136 mm SL.

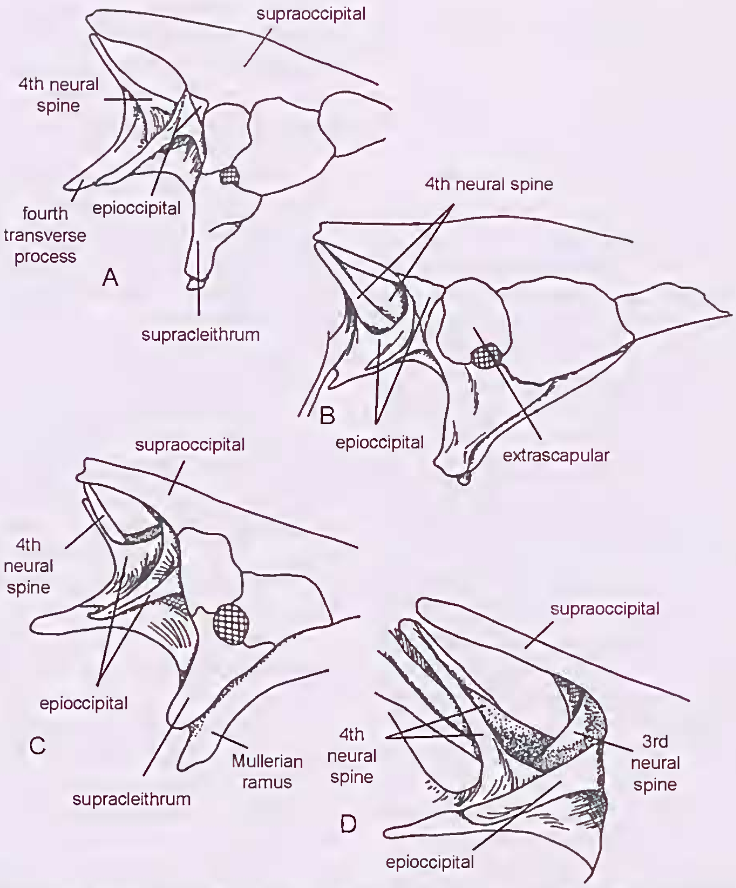

Fig. 6. Fourth neural spine and epioccipital flange in some ariids: **A**, *Netuma proximus*, 158 mm SL; **B**, *Aspistor hardenbergi*, 60 mm SL; **C**, *Nemapteryx armiger*, 176 mm SL; **D**, *Nedystoma dayi*, 158 mm SL.

a median lamina extending from the ventral surface of the supraoccipital.

The plesiomorphic condition for these four groups appears to be low ridges or laminae, a feature present in diplomystids, †*Hypsidoris* and many other catfishes. Howes (1985) remarked that the space between the cranium and the fourth neural spine has almost disappeared in advanced siluroids. Lundberg and McDade (1986) and Ferraris Jr (1988) reported that the elevated lamina is also found in some pimelodids and bagrids, and my outgroup material supports these observations; while the laminae are low in *Synodontis* and *Pimelodus*. In doradids, only conditions 1) and 2) seem to be present – not the epioccipital, condition 3). *Rita* (Bagridae) has a very high transverse ridge.

Lundberg (1982) implied that the vertical lamina is a phenomenon associated with large species size (i.e., for strength) but this supposed correlation is not supported in the Ariidae where it occurs in taxa attaining quite a range of maximum sizes (e.g., from *Nedystoma dayi* to *Netuma thalassinus*); neither is it evident in some taxa with thicker and heavier bones (e.g., *Batrachocephalus*).

State 0 = low ridges or laminae; 1 = moderately elevated ridges; 2 = well-elevated to high laminae or flanges.

13. *First pharyngobranchial.* There are four separate, ossified pharyngobranchials of similar length in the Diplomystidae (Arratia 1987) and *Rita* (pers. obs.): this is the supposed primitive condition. Many catfish families have three pharyngobranchials (e.g., Schilbeidae (Tilak 1964), some Bagridae (Tilak 1965a; Skelton 1981)) and others have two (e.g., some Plotosidae (Tilak 1963), Sisoridae (Tilak 1963a), Amblycipitidae (Tilak 1967), Trichomycteridae (Arratia and Menu-Marque 1984), Loricariidae (Schaefer 1987) and Chacidae (Brown and Ferraris Jr 1988)). Of the outgroup material, *Rita* and *Neosilurus* have a long, basally situated first pharyngobranchial and a cartilaginous second pharyngobranchial. The Pimelodidae have a similar second pharyngobranchial, but the first pharyngobranchial in *Pimelodus* is long

and situated midway along the epibranchial, in *Rhamdia* it is short and at the epibranchial angle. The position of the first pharyngobranchial has systematic importance in the Pimelodidae (F. Mago-Leccia pers. comm.). The Doradidae appear to lack the first pharyngobranchial and often the second, which is cartilaginous (C. Ferraris Jr, pers. comm.).

Most ariids have three pharyngobranchials: the first elongate (ovate in the group of species including *Plicofollis* n. gen. *argyropleuron*), lying parallel and dorsal to the first epibranchial; the third rectangular to 'v'-shaped, lying between the second and third epibranchials; the fourth almost square, between the third and fourth epibranchials and forming a base for the tooth plate. I could not distinguish easily an autonomous second pharyngobranchial between or before the contiguous cartilaginous ends of the first two epibranchials in any ariids I examined, but it may be present in *Bagre marinus* (pers. obs.). The position of the first pharyngobranchial varies in the ariids and a trend to lose this element is evident. Expressions of this character similar to those in the Ariidae appear to have arisen independently within the siluroids.

State 0 = first pharyngobranchial situated close to distal end of epibranchial; 1 = first pharyngobranchial situated along shaft of epibranchial or near epibranchial angle; 2 = first pharyngobranchial missing or united with epibranchial at its expanded angle.

14. *Posterior cleithral process.* The posterior cleithral process (or 'humeral process') is present and well-developed in diplomystids, ictalurids (Lundberg 1982), bagrids, †*Hypsidoris*, other 'diverse neotropical catfishes' (Stewart 1986: 669) and the auchenipterids and doradids (Curran 1989). In †*Hypsidoris* it is long and ornamented (Grande 1987; Grande and de Pinna, 1998); in *Rita* and *Bagrichthys* the process is very large (Bhimachar 1933; pers. obs.); in †*Astephus* (Ictaluridae) it is long and sculptured (Grande and Lundberg 1988); in the doradids and mochokids I examined it is long and smooth or tuberculated. The pimelodids, *Schilbe*, plotosids, silurids and *Pangasius* have a medium to short process. In *Brochis* and *Dianema* (Callichthyidae) the process is very extensive.

The long and unornamented form of the posterior cleithral process is probably the most plesiomorphic condition (Lundberg 1982), being common among catfishes (see above). Lundberg believed that alternative conditions are derived independently (and see Bailey and Stewart 1984).

Most ariids have a moderately large, often rugose posterior cleithral process, usually anteroventrally thickened; although in some (e.g., *Netuma*) it is somewhat broad. The extremes are displayed in *Cinetodus froggatti* where it is very long, almost horizontal and strong, and *Nedystoma dayi* and *Cathorops* where it is very short. In some taxa (e.g., cf. *Arius harmandi*) the process is striated, and in others (e.g., *Arius leptonotacanthus*) it is rough and pitted. In *Galeichthys* the posterior cleithral process is fan-shaped.

State 0 = process long; 1 = process moderately long; 2 = process fan-shaped; 3 = process short.

15. *Eye covering.* Arratia (1987) cited examples of siluroids having either covered or naked eyes and observed that the traits can vary within the one family. The diplomystids have a naked eye as do most ariids and most bagrids but some pimelodids lack a free eye margin (Gosline 1941; Mees 1974; Stewart 1986a; Lundberg *et al.* 1991); as do the silurid and doradid taxa in my outgroup material. Bailey and Stewart (1984) concluded that the loss of a free orbital rim in the African bagrid *Bathybagrus* was apomorphic.

The primitive ostariophysan condition is one of a free orbital rim (Lundberg 1982; Lundberg and Mago-Leccia 1986) and the covered eye of several unrelated lineages probably has developed in response to habitat preference. For ariids, I concur with these opinions. However, the fallibility of proposed phylogenetic relationships are demonstrated in the Siluridae, in which Kobayakawa (1989) considered the covered eye as plesiomorphic as that is the condition in her outgroup of Bagridae, Ictaluridae and Plotosidae, while Bornbusch (1995) considered that a free orbital rim represents the plesiomorphic condition in the same family.

State 0 = naked eye – free (or almost) orbital rim; 1 = subcutaneous eye.

16. *Extent of gill opening.* Several character states are exhibited by the Ariidae in the freedom of the branchiostegal membrane and the extent of the gill opening. In some taxa (e.g., *Hemiarius dioctes, Nedystoma novaeguineae, Brustiarius nox*) the gill openings extend well forward on the isthmus, the branchiostegal membrane margins are broad and free, meet medially in an acute angle, or overlap. In other taxa (e.g., *Ariopsis graeffei, A. leptaspis, A. felis*) the openings are moderately wide and the broad, free membranes meet on the isthmus at approximately a right angle; or they may form an obtuse angle or concave fold. The third state (in, e.g., *Cinetodus froggatti, Amissidens* n. gen. *hainesi, Nedystoma dayi, Ketengus typus*) is where the gill openings extend only to the sides of the isthmus or slightly further with the narrow-margined membranes joining broadly across the isthmus, or the membranes folding into the isthmus.

Gosline (1973) discussed and contrasted the opercular 'sleeve's' function during inspiration and expiration in large-mouthed and smaller mouthed catfishes. The conditions he described occur in the Ariidae where the size of the gill openings is well-correlated with head height and mouth width.

The usual plesiomorphic condition among catfishes is of an unrestricted gill opening. Lundberg (1982) observed that branchiostegal membranes fusing with each other across the throat is an apomorphy, but one which has arisen independently in several catfish lineages, such as doradids, auchenipterids, callichthyids and aspredinids (Alexander 1965; Mees 1974; pers. obs.). Armbruster (1998) however, considered that restricted gill openings are plesiomorphic in the loricariids. I consider a restricted gill opening the advanced condition in the Ariidae.

State 0 = wide gill openings, branchiostegal membranes meeting well forward, overlapping; 1 and 2 = moderately wide or less wide gill openings, membranes meeting at an acute or obtuse angle (concave); 3 = restricted gill openings.

17. *Buccopharyngeal pads or flaps. Nedystoma dayi* is distinguished in systematic literature partly by the large pads or flaps hanging from the rear of the buccal cavity and attached to the posterodorsal aspect of the anterior gill arches. Roberts (1972, 1978) observed that such structures function very effectively in straining and sorting fine food items, especially in the mid-water column. Lundberg *et al.* (1987: 81) drew attention to the 'additional advanced features' of the feeding apparatus in the planktivorous gymnotid *Rhabdolichops zareti* which appear to be homologous with the structures present in *Nedystoma dayi*, viz: fleshy, suspended pads and valves on the gill arches and buccopharyngeal roof. *Rhabdolichops zareti* occupies swiftly flowing waters, has numerous gill rakers and a quadrangular mouth gape. The planktophagous catfish *Hypophthalmus edentatus* has such structures (Roberts 1972) as has the pimelodid *Rhamdia*. Vari (1989) noted the numerous, probably functionally homologous, lobulate protruberances extending from the mouth in some curimatids (Characiformes) and supposed that these structures can promote an increase in the amount of buccal mucus, an adaptation possibly correlated with the species' microphagous and detritivorous diet.

Retention of well-developed pads and flaps in ariid taxa at adult stadia appears to be derived. Whereas the majority of ariids have moderately developed pad structures, a handful have flaps substantially identical to those in *N. dayi*, and some have convoluted flaps and extensions on the upper gill arches which almost certainly function in a similar manner. *Amissidens* n. gen. *hainesi*, *Brustiarius nox*, *Cathorops hypophthalmus* and cf. *Arius acutirostris* are examples. In *Cephalocassis melanochir* the large pads have scalloped margins. In some taxa, pads are moderately developed at juvenile stadia and much reduced in adults, with such structural changes probably correlated with a change in dietary preference from finer to larger food items. In some ariids (e.g., *Osteogeneiosus, Galeichthys, Guiritinga barbus, Genidens*) the lower inside of the operculum bears a deep pocket or pouch, and in them (and some other taxa such as *Cochlefelis burmanicus* and *Galeichthys*) the gill membrane is broadly attached to the lower inside operculum. Perhaps these features have a function similar to the enlarged buccopharyngeal structures.

State 0 = gill arch pads and buccopharyngeal flaps low or poorly developed at adult stadia; 1 = pads and flaps of moderate size in adults; 2 = pads and flaps large and fleshy in adults.

18. *Mesethmoid shape.* The plesiomorphic shape of the siluroid mesethmoid is elongate and 'T'-shaped, usually with a median notch (Tilak 1965; Lenous 1967; Howes 1983; 1983a; Arratia 1987; others) or excavation (e.g., in *Schilbe*). This form is present throughout the Siluriformes. The lateral arms, or cornuae, can be exceedingly produced (e.g., *Trogloglanis* – Lundberg 1982; Chacidae – Brown and Ferraris Jr 1988). Ariids lack the mesial processes on the cornuae present in ictalurids and 'various catfishes in other families' (Lundberg 1982: 31) which is a derived condition among catfishes.

Howes (1983) described several derived states of the siluroid mesethmoid and most of these states are exhibited in the Ariidae. There is a trend in the group towards loss of the median notch and a general broadening of the mesethmoid. The more conservative form is a mesethmoid having a moderately wide neck and anterior cornuae diverging at approximately right angles, separated by a deep median concavity; and the smooth ventral surface of the cornuae articulating with the dorsal surface of the premaxillaries (Fig. 7). In contrast, some taxa (e.g., *Nedystoma novaeguineae*) have an expanded, convex mesethmoid without a

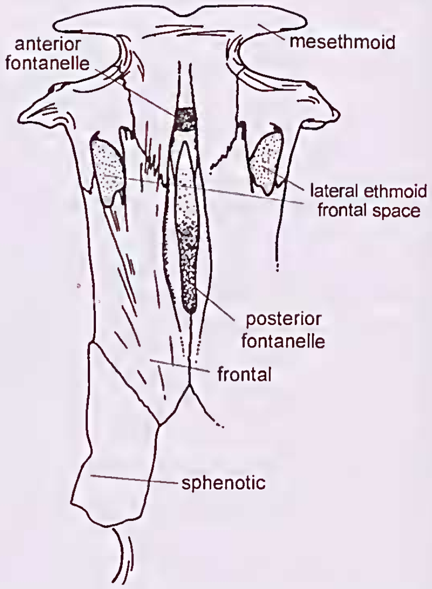

Fig. 7. Dorsal view of anterior part of skull of *Ariopsis leptaspis*, 162 mm SL.

median notch; others (e.g., *Plicofollis* n. gen. *dussumieri*) have a broad mesethmoid with very shallow notch or none. In *Netuma thalassinus* and *Hemiarius grandicassis* the termination is convex and fluted or ridged while in cf. *Arius macrorhynchus* the short cornuae are partly enveloped in a median, convex, heavily striated prominence turned ventrad; in them the median notch also is lacking. I interpret these conditions as apomorphic. Another derived condition is where the ventral mesethmoid surface becomes concave with ontogeny (e.g., in *Cochlefelis spatula* and *Hemiarius insidiator*).

State 0 = divergent cornuae with median, deep notch; 1 = divergent broader cornuae with medium or shallow notch; 2 = broad cornuae; mesethmoid anterior margin slightly convex to truncate with only remnant of a notch; 3 = convex, broad mesethmoid; 4 = prominent and blunt apex, cornuae reduced; bone creased transversely; 5 = prominent and rounded apex, cornuae broad; margin of bone fluted.

19. *Nasal bone shape.* The nasals are simple, slender tubes in †*Hypsidoris*, the Diplomystidae (Arratia 1987) and many other catfishes (Lundberg 1982; pers. obs.). Simple tubes, often broader anteriorly where they tend to bifurcate, and lying longitudinally on the cranium, appear to represent the plesiomorphic condition in the ariids. This condition is exhibited by *Arius arius*, although anteriorly the nasals are turned outward. It is general within the Ariidae. However, there is a trend for the nasals to lie over or cradle into the mesethmoid margin (e.g., *Bagre marinus*), most apparent in those taxa where that bone is broader. The expanded, irregular nasal form in *Nedystoma novaeguineae*, *Batrachocephalus* and, to a lesser extent *Hemiarius insidiator*, is further derived, and in cf. *Arius macrorhynchus* the nasals have a distinct, irregular shape.

State 0 = simple and straight longitudinal tube, slightly expanded anteriorly; 1 = curved tube, tending to parallel the curve of the mesethmoid neck and/or slightly bifurcate anteriorly; 2 = irregularly shaped or very broad anteriorly or strongly bifurcate.

20. *First infraorbital (lachrimal) shape.* In *Trichomycterus* the lachrimal (the anterior-most bone of the infraorbital series) is simple (Arratia and Menu-Marque 1984). The same condition was recorded in *Malapterurus* by Howes (1985) and diplomystids by Arratia (1987), suggesting that this form has been independently derived in several lineages. Apomorphies are exhibited in other siluroids: for example *Rhamdia* has an elongate lachrimal; the lachrimal in doradids is considerably enlarged and irregularly-shaped; and in *Neosilurus* the lachrimal is broadly crescentic or moon-shaped. The characteristic and presumably plesiomorphic form in many siluroids (Howes 1983; Schaefer 1987) is a generally rhombic or 'axe'-shaped lachrimal with anterior and posterior processes well produced.

The usual condition is exhibited in *Arius arius* where the lachrimal is a simple, oblong plate with triangular processes diverging from each corner (Fig. 8). In several taxa, however (e.g., *Nedystoma novaeguineae, Bagre marinus, Batrachocephalus*) the lachrimal is more ornate in shape, representing derived conditions.

State 0 = rhombic, with well-produced angles; 1 = flattened, angles extremely produced; 2 = rectangular with few obtuse angles; 3 = simple, irregular or crescentic.

21. *Shape of the vomer.* A 'T, or arrow-shaped vomer is present in many siluroids, including †*Hypsidoris* (Lundberg 1982; Grande 1987; Grande and Lundberg 1988; pers. obs.) while a rhombic, enlarged vomer is a unique derived feature of the Diplomystidae (Arratia 1987). Vomer size varies and in some groups, (*Hypophthalmus* (Howes 1983) and loricariids (Schaefer 1987)), it may be needle-like with or without greatly reduced lateral arms. In the Helogeninae (family Cetopsidae) its posterior process is reduced or absent (de Pinna and Vari 1995).

In the ariids, the vomer is usually 'T'-shaped (Fig. 9). In *Arius arius* the head of the vomer is triangular: the short arms are deeply indented distally and the posterior extension is long. Variations around this form are common (e.g., the arms are slightly abbreviated, or long (*A. manillensis*), the 'head' of the bone is dentate, or the head and arms form a wedge (*Cephalocassis melanochir, Cryptarius* n. gen. *truncatus*) but probably

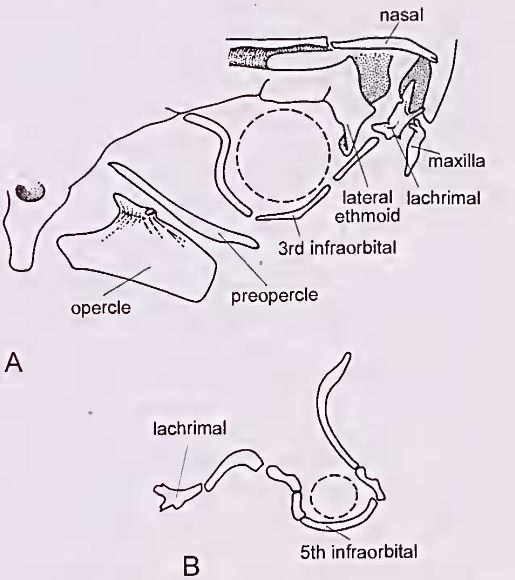

Fig. 8. Infraorbital series of **A**, *Netuma thalassinus*, 127 mm SL; and **B**, *Nedystoma novaeguineae*, 150 mm SL, LHS. Dashed lines indicate position of eye.

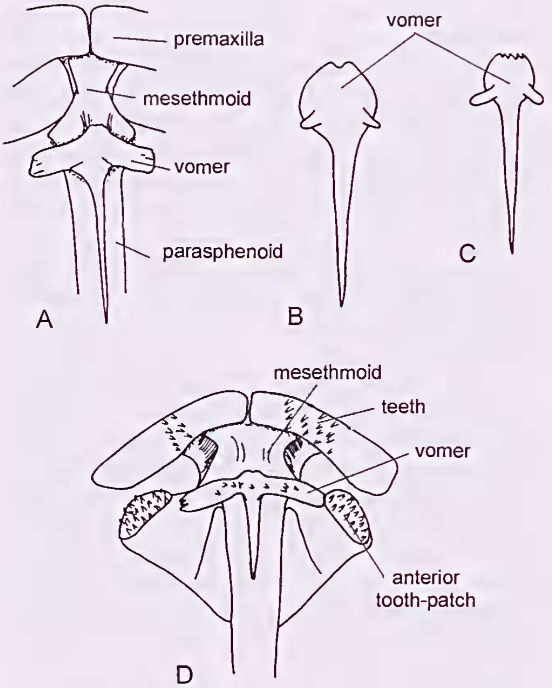

Fig. 9. Vomer shape in **A**, *Arius arius*, 112 mm SL; **B**, *Plicofollis* n.gen. *argyropleuron*, 70 mm SL; **C**, *Plicofollis* n.gen. *argyropleuron*, 162 mm SL; **D**, *Hemiarius dioctes*, 90 mm SL.

do not represent independent character states. However, the general 'T' condition is lacking in the group of species including *Plicofollis* n. gen. *nella* and *P.* n. gen. *polystaphylodon*, and in them the head is enlarged and rounded and the arms are very short. I consider this 'club'-shaped condition apomorphic.

State 0 = 'T'- shaped + variations; 1 = conical head, arms much reduced.

22. *Mandibulary pores.* The openings of the mandibulary sensory canal lie along the anteroventral aspect of the mandible. Lundberg (1982) believed that there are six openings primitively, and that higher counts are derived. The foramina ('pores') can be clearly seen on †*Hypsidoris* and †*Asteplus*; and Arratia (1987) illustrated those in *Diplomystes*. Pores appear to be absent from the loricariids (Schaefer 1987). In *Prietella* (Lundberg 1982), plotosids and some bagrids the pores are large (pers. obs.) and they are small in *Synodontis*, some pimelodids, *Parasilurus* and *Schilbe*.

Ariids display variability in the number (four to eight) and size of the pores, which are present only in the mandible. However, because I experienced difficulty in counting the pores nearest the symphysis in some osteological preparations due to bone convolutions, I cannot arrive at a real pore number for each ariid taxon examined. However, the *size* of the foramina can be used in phylogenetic reconstruction. Some ariid taxa (such as *Nemapteryx armiger*, *Hemiarius dioctes*, *Nemapteryx augustus*, *Nedystoma novaeguineae*, *Bagre* and *Sciades troschelii*) have noticeably large openings at all growth stadia, whilst others (such as *Ariopsis felis*, *Arius manillensis*, *Cochlefelis danielsi* and *Cinetodus carinatus*) have quite small (or no?: *Batrachocephalus*) openings. Bornbusch (1995) decided that larger pores represent the derived condition in the Siluridae. The reverse appears to be true for the Ariidae.

State 0 = (very) large openings; 1 = moderate-sized openings; 2 = very small or concealed openings.

23. *Epioccipital plus extrascapular.* The epioccipital lamella extends well posterior to the skull in all ariids except for *Galeichthys*. In many ariid taxa (including *Arius arius*), the proximal part of the bone – which forms a major portion of the posterior wall of the neurocranium – closely underlies or articulates with the underside of the extrascapular and the posterolateral arm of the supracleithrum (Fig. 10). In several ariids however (e.g., *Netuma proximus*, *Aspistor hardenbergi*, *Plicofollis* n. gen. *polystaphylodon*, *Hemiarius sona*, *Cryptarius*

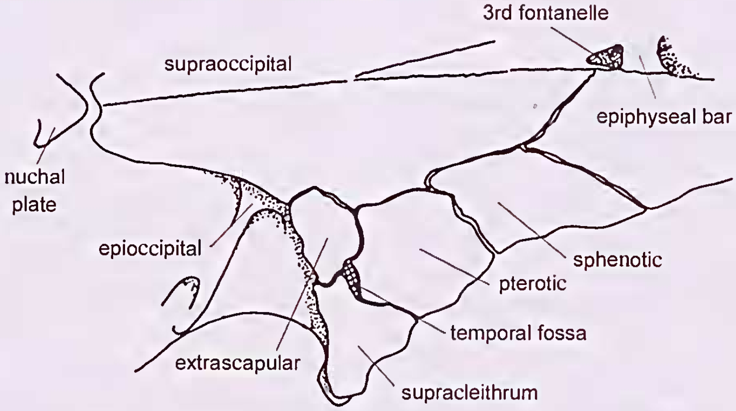

Fig. 10. Posterolateral view of neurocranium of *Arius arius*, 190 mm SL, showing separate extrascapular.

n. gen. *truncatus, A. planiceps, Sciades parkeri, Bagre marinus*) the epioccipital invades the skull roof as an *additional* dermal skull bone: i.e., it is exposed, forms part of the neurocranium, and that portion matches the ornamentation of the other dermal bones. No other catfishes (or ostariophysans) have the epioccipital invading the skull roof, besides retaining the extrascapular, and I consider this condition derived.

State 0 = epioccipital not in skull roof; 1 = epioccipital invading skull roof.

24. *Epioccipital minus extrascapular.* The status of the plate-like bone between the supraoccipital and the supracleithrum has often been debated (Lundberg 1975a; Grande 1987; also Howes 1985). It is usually present in the diplomystids (Arratia 1987) and at least nine other catfish families including Mochokidae, Bagridae, Ariidae and Doradidae. There is a pronounced trend towards its division (e.g., in some ictalurids: Lundberg 1975a; 1982) or independent loss (Arratia 1987) within the siluroids.

Whereas in most ariids the extrascapular is well-developed and clearly identifiable, in at least two groups of ariids the extrascapular has amalgamated with the anterior portion of the epioccipital which is thus exposed and becomes an element of the skull roof (cf. Character 23) (Fig. 11). Lundberg (1975a) and Curran (1989) reported a similar situation for the doradids and auchenipterids; i.e., in them the extrascapular is 'replaced' by the intrusive and dominant epioccipital which abuts the supracleithrum and pterotic on one side, and the second nuchal plate on the other. Some of the ariids possessing the exposed and dominant epioccipital have highly ossified skulls posteriorly, and all have high flanges on the epioccipital extension and the neural spine. It is possible that the amalgamation of the two bones acts to reduce weaker sites in the skull (as, for e.g., at sutures) in response to achieving strength in that area.

State 0 = extrascapular apparent; 1 = extrascapular amalgamated with epioccipital.

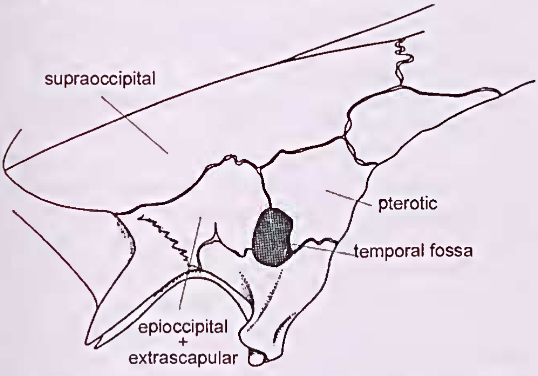

Fig. 11. Posterolateral view of neurocranium of *Cinetodus carinatus*, 122 mm SL. Extrascapular is fused with epioccipital.

25. *Temporal fossa.* Many ariids possess a large fossa at the intersection of the supracleithrum, pterotic and extrascapular. Such a fossa is not common in catfishes, at least in adults where, if it is present, it is largely overlain by the extrascapular. However, pangasids, schilbeids, some sisorids and diplomystids also have a fossa (Bhimachar 1933; Tilak 1963a, 1964; pers. obs.). I consider the presence of the temporal fossa in adult ariids as plesiomorphic because: a) it is rare in the siluroids and present in the characoids (and some cyprinoids) (Roberts 1973) it is much reduced or even absent in some ariids, especially at adult stadia; and c) it indicates the space between the neurocranium and pectoral girdle in taxa where the supracleithrum is only ligamentously attached or where both arms of the supracleithrum are not strongly sutured to the skull (e.g., in *Schilbe* and some ariids including *Ariopsis robertsi*). Howes (1985) considered a loose connection of the supracleithrum and neurocranium to be apomorphic.

State 0 = fossa large and (moderately) prominent at all growth stadia; 1 = fossa smaller, much reduced, or absent (especially in adults).

26. *Metapterygoid position.* With the substantial reduction of the ectopterygoid and the mesopterygoid in catfishes, the metapterygoid has moved forward to occupy the space they vacated and, in turn, the hyomandibular has extended anteriorly to fill the space left by the forward movement of the metapterygoid. This condition exists in many taxa (e.g., diplomystids, ictalurids, many bagrids, pimelodids, †*Hypsidoris*, schilbeids, *Clarias*, some sisorids, doradids and ariids).

In many siluroids, the posterior margin of the metapterygoid lies above or before (well before in pimelodids and *Chrysichthys*) the middle of the quadrate. Some ariids, however (such as *Hemiarius dioctes, Amissidens* n. gen. *hainesi, Plicofollis* n. gen. *argyropleuron, Potamarius* and *Osteogeneiosus*) have a somewhat enlarged metapterygoid where the hind border extends posteriorly to lie in line with the hind border of the quadrate – or even beyond it (Fig. 12). The condition in *Malapterurus* is an extreme example (Howes 1985). A general elongation of the suspensorium in the region between the articular condyle for the quadrate and the hyomandibular accompanies the posterior progression of the metapterygoid (see also Ferraris Jr 1988: *Nemuroglanis*). I consider the posterior position of the metapterygoid as derived, although it mirrors the gonorhynchiforms (Fink and Fink 1981).

Additional apomorphies are that in *Bagre marinus*, for example, the metapterygoid is high, and expanded (its posterior border slightly behind the quadrate); in *Cathorops fuerthii*, the hyomandibular bears a ridge; and in *Ariopsis felis, Potamarius* and *Aspistor kessleri* the hyomandibular is elongate.

State 0 = metapterygoid well before middle of quadrate (e.g., outgroup, pimelodids); 1 =

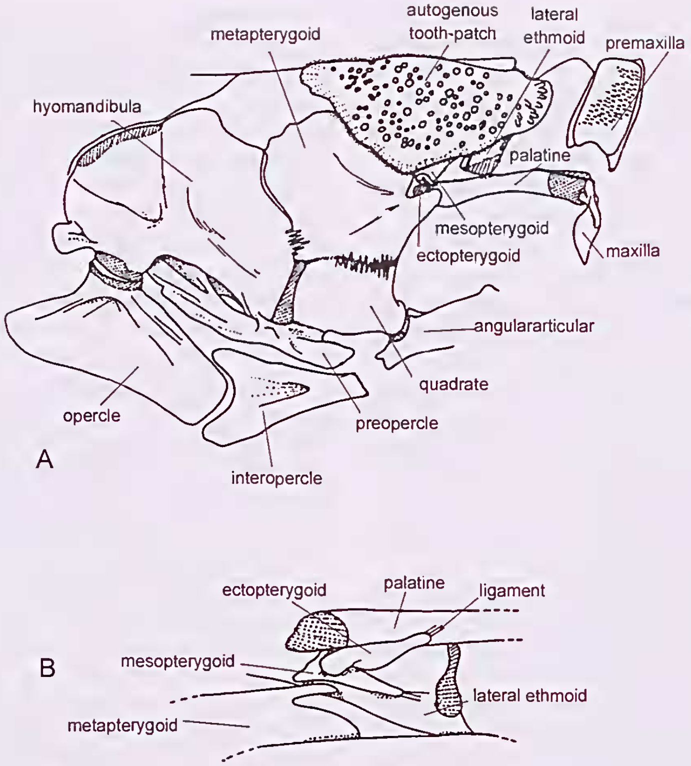

Fig. 12. Mesial oblique view of suspensorium of **A**, *Arius arius*, 190 mm SL; **B**, enlarged view of palatine region of *Arius arius*, 112 mm SL.

metapterygoid hind margin above middle of quadrate; 2 = metapterygoid hind margin in line with hind margin of quadrate; 3 = metapterygoid hind margin well behind hind margin of quadrate.

27. *Metapterygoid – hyomandibular suture.* In the Ariidae the metapterygoid is roughly square and sutures to the quadrate ventrally and to the hyomandibular posteriorly. The breadth of the sutures varies in the Ariidae from being very broad (e.g., *Batrachocephalus, Ketengus*) to narrow (e.g., *Bagre marinus*). Such variation was also observed by Brown and Ferraris Jr (1988) in the Chacidae and by Bornbusch (1995) in the Siluridae. A broad suture extending the length of the hyomandibular-metapterygoid interface is widespread in catfishes (present in, for example, †*Hypsidoris, Diplomystes* (Fink and Fink 1981), †*Astephus* and other ictalurids (Lundberg 1982) and some Chacidae) and is considered to be the plesiomorphic condition. In *Cephalocassis melanochir* and *Bagre marinus* the hyomandibular-quadrate-metapterygoid interfaces are represented by extensive (symplectic?) cartilage.

State 0 = broad suture; 12 = moderately wide suture; C = short suture.

28. *Skull ornamentation.* Primitively, much of the dorsal surface of the catfish skull is covered with heavy exostosis – of sharp or blunt tubercles, ridges, granules, grooves and rugae (Stewart 1986; Grande 1987). The families in which strong ornamentation of the skull is exhibited are the Ariidae, Bagridae, Pimelodidae, Doradidae, Auchenipteridae, Sisoridae and Clariidae; also *Synodontis* (Mochokidae) and *Neosilurus* (Plotosidae) (pers. obs). †*Hypsidoris* species have a heavily ornamented neurocranium (Grande 1987; Grande and de Pinna 1998) as has the ictalurid †*Astephus* (Grande and Lundberg 1988). Many Characiformes also exhibit strong skull ornamentation (Lundberg 1975).

Ornamentation continued to the skull roof above the hyomandibular occurs because the cheek muscles (adductor mandibularis) are restricted to the cheek, as in most ostariophysans and lower teleosts (Grande and Lundberg 1988). Smooth bone surfaces (representing extensive cranial attachment of jaw muscles) have probably evolved independently in several catfish lineages, and are evident in the ariid genus *Galeichthys* (for example). Even so, there is consistent variation in the relative smoothness of the cranial surface among the ariids, unrelated to cheek musculature, and I am not convinced that a highly granulated or rugose dorsal skull surface represents the plesiomorphic conditions: perhaps that condition (such as in *Hemiarius sona, Hexanematichthys mastersi, Ariopsis guatemalensis, Sciades emphysetus*) and very smooth skulls (such as in *Bagre, Ketengus, Nedystoma dayi, Cephalocassis melanochir*) are independent apomorphies.

I recognise three states for this character despite some problem with accounting for ontogeny and intraspecific variation and the difficulty of unequivocally describing the ornamental diversity exhibited in the Ariidae.

State 0 = granular or tuberculated or rugose skull surface; 1 = smooth to striate; 3 = smooth.

29. *Shape and position of the adipose fin.* Alexander (1965) discussed the compensatory values of large and small adipose and anal fins, the former seemingly useful in swim stability. The usual form and position of the adipose fin in catfishes are of a moderately high and free fin smoothly rounded posteriorly, situated approximately over the middle of the anal fin. There is considerable variability in the size and position of the adipose fin in the Ariidae. The long-based adipose fin possessed by some ariids (e.g., *Cinetodus froggatti, Cochlefelis spatula, Aspistor hardenbergi*) is also common to a number of 'generalised' catfishes including the diplomystids, †*Hypsidoris* (Grande 1987), bagrids, many pimelodids (Alexander 1965; Stewart 1986a; pers. obs.) and *Ancharius*. I consider this condition plesiomorphic. The derived condition – of a small-based adipose fin situated above the posterior half of the anal fin – is exhibited in the sea-inhabiting *Netuma* and several freshwater taxa such as *Brustiarius nox*.

Other authors (e.g., Mees 1974; Fink and Fink 1981; Howes 1983; Skelton 1984; Ferraris Jr and Fernandez 1987; Curran 1989) generally have considered the small-based, posteriorly situated fin to be derived.

State 0 = long-based adipose fin equal or subequal to length of anal fin base (length 7–22 [mean 15]% SL); 1 = moderately long-based adipose, over middle or anterior third of anal fin (length 6–16 [mean 10]% SL); 2 = short-based adipose, over (middle), posterior half or third of anal (length 3–12 [mean 6.5]% SL).

30. *Barbel number.* The number and situation of sensory barbels in catfishes appears to be haphazard and opinions vary concerning their phylogenetic information. Lundberg and Baskin (1969), Roberts (1973) and Fink and Fink (1981) considered the primitive form to be possession of a maxillary pair of barbels only; Curran (1989: Auchenipteridae) and Bornbusch (1995: Siluridae) considered that a reduction in the number of mental barbels was the derived condition; and Howes (1983: Hypophthalmidae) and Kobayakawa (1989: *Silurus*) thought the opposite.

Possession of only maxillary barbels is not a state singular to the primitive diplomystids however, as it occurs also in the phylogenetically more advanced loricariid group. Howes (1985) believed that possession of nasal barbels may be plesiomorphic: present (e.g.) in schilbeids, *Malapterurus*, plotosids, *Clarias*, some bagrids and *Anadoras* species. I incline to Fink and Fink's view (1981) that barbels other than the maxillary barbels have been independently derived within the Siluriformes; and, further, that a barbel complement other than six (a pair of maxillary, mandibulary and mental) is derived within the Ariidae. The South-east Asian taxon *Batrachocephalus* has a pair of mandibulary barbels only and *Osteogeneiosus* has a pair of maxillary barbels only. *Bagre bagre* and *B. marinus* lack mental barbels. *Ancharius* has a pair of short and thin nasal barbels, a feature unknown in any ariid and *Ancharius brevibarbis* has fringed barbels (pers. obs.), another unknown ariid feature.

State 0 = 3 pair (maxillary, mandibulary, mental); 1 = 1 pair (maxillary only); 2 = 1 pair (mandibulary only); 3 = 2 pair (maxillary and mandibulary); 4 = 4 pair (outgroup); 5 = 3 pair (nasal, maxillary, mandibulary).

31. *Barbel position.* The matter of barbel homology within the Ostariophysi has been discussed by several authors (e.g., Roberts 1973; Fink and Fink 1981; Arratia 1987) and Alexander (1965) and Gosline (1975) interpreted the movement and function of the barbels in different ostariophysans. However, the position of the mandibular barbel bases is worthy of attention. Albeit in the majority of catfishes the barbel bases are 'moderately' separated and staggered, in some ariid taxa (e.g., *Arius hainesi*; also in some pimelodids: Howes 1983 and Stewart 1986) the barbel bases lie close together near the mandibulary symphysis and are approximately transversely aligned, and in others (e.g., *Hemiarius stormii*) the barbel bases are well-separated, spread along the chin line, and staggered. Such variations from the general condition (above) appear to be derived. Indeed, Curran (1989) noted that three auchenipterid genera have four mental barbels in a transverse series on the chin (along with some members of the Heteropneustidae and Pimelodidae, also Doradidae, Callichthyidae and Loricariidae). Contrary to Curran's decision to exclude this character from analysis because of homoplasy, I consider it makes a worthwhile contribution to ariid phylogenetic analysis.

State 0 = bases close together, aligned (or almost), near symphysis; 1 = bases moderately separated, slightly staggered; 2 = bases widely separated, laterally on mandible, well staggered.

32. *Lateral line at tail base.* The form of the lateral line at the tail base in catfishes appears to be stable. A lateral line curving slightly either dorsally or ventrally at the tail base is probably the plesiomorphic condition, as it is present in this form in diplomystids (Arratia 1987). In some ariids however, the lateral line turns sharply dorsad; and in some other ariids (e.g., *Netuma thalassinus, Osteogeneiosus, Arius jatius, A. malabaricus, Cochlefelis burmanicus, Bagre bagre*) the lateral line bifurcates at the tail base. This apomorphy also occurs in other catfishes such as the pangasids,

schilbeids, some sisorids, pimelodids, auchenipterids, some doradids, *Hypophthalmus* and *Cranoglanis* (Lundberg and Baskin 1969; pers. obs.) as well as in the chanoid *Gonorhynchus* (Lundberg and Baskin 1969).

Bleeker (1858) partly based his genus *Hemipimelodus* on the bifurcate nature of the lateral line. Interestingly, *H. borneensis* exemplifies a condition not uncommon in ariids – that of the lateral line bifurcating in some individuals and simply turning upwards in others.

State 0 = lateral line slightly curved one way at tail base; 1 = lateral line sharply turned up at tail base; 2 = lateral line bifurcate at tail base.

33. *Shape of the swim bladder.* The plesiomorphic catfish swim bladder is large and sac-like or 'heart'-shaped, with smoothly rounded margins (Alexander 1964; Stewart 1986) and covered with a silvery peritoneal tunic. Fink and Fink (1996) affirmed that the siluriform swim bladder comprises an anterior and a posterior chamber, even though an external constriction between the chambers is absent (a partial transverse septum separates the two parts of the bladder). In most ariids, the posterior chamber (section) is further divided by two or more irregular pairs of incomplete septae linked to a median longitudinal partition. Alexander (1964, 1965) noted that the shape of catfish swim bladders is maintained by the internal partitions, and Tavolga (1962) surmised that the ariids use the septae for channelling sound.

An additional third chamber connected by a ductus pneumaticus to the second (posterior) chamber is present in several siluroid groups such as *Pangasius* and *Malapterurus*, possibly some pimelodids (Roberts 1973; Howes 1985; Stewart 1986), *Rita* (pers. obs.) and *Sciades* (Ariidae) and probably represents the plesiomorphic condition.

In some ariid taxa (e.g., *Aspistor kessleri*) the bladder is almost rounded; in most (including *A. arius*) it is heart-shaped or ovate, and in others (e.g., *Ketengus*) it is almost triangular. The edges or sides of the swim bladder are usually smooth and entire but in some taxa the sides are deeply creased internally (e.g., *Plicofollis* n. gen. *nella*, *P.* n. gen. *polystaphylodon*), deeply scalloped externally (e.g., *Hemiarius dioctes, Netuma proximus, N. bilineatus, Osteogeneiosus*), or creased/scalloped internally and externally (e.g., *Plicofollis* n. gen. *argyropleuron*). This last condition is also found in some pimelodids (Stewart and Pavlik 1985; Stewart 1986) and is derived. A long and oval, board-like swim bladder internally divided by numerous septae is an autapomorphy of *Hemiarius insidiator*. Howes (1983) noted a trend for the more derived siluroids (e.g., loricariids, callichthyids, trichomycterids) to have reduced and encapsulated swim bladders (also Sisoridae: Roberts and Ferraris Jr 1998), a trend directed towards a demersal existence (Alexander 1965) wherein a greater variety of environments can be exploited (see Gee 1976). The larger, high-volumed swim bladder hence appears to represent the plesiomorphic condition.

As the Weberian apparatus functions to transmit vibrations from the bladder to the inner ear, the form of the bladder must either a) have some effect on the type of vibrations transmitted, b) provide efficient reception of sound vibrations from the preferred habitat of different taxa, or c) have no effect. Correlation between bladder shape and volume, vibrations type and strength and habitat preference could be revealed with further study.

Under this heading I make the following observations: (1) during immature growth stadia, most ariids, whatever the swim bladder volume, inhabit the lower water column. As the body tissue of ariids becomes increasingly buoyant from oil and fat deposition as growth proceeds, adults are more common higher (even just a little higher) in the water column; and (2) compensation of the effect of low swim bladder volume can also be achieved by active swimming, a phenomenon observed in juvenile ariids, at least.

State 0 = internal and external swim bladder edges smooth; 1 = internal swim bladder edge creased, external edge smooth; 2 = internal swim bladder edge smooth, external edge moderately to deeply scalloped; 3 = internal and external swim bladder edges creased or scalloped.

34. *Pads on the pelvic fins.* A noticeable feature of female ariids is the gradual thickening of the sixth (and occasionally fifth) ventral ray with advancing sexual maturity. Rimmer (1985), working with *Ariopsis graeffei*, was able to demonstrate that the pads develop synchronously with ripening of ova and regress post-spawning (see also Lee 1937; Smith 1945). Sometimes the pads are distinctively shaped – as in *Amissidens* n. gen. *hainesi* and some *Cathorops* species. Day (1877: 457) observed that the pelvic rays are thickened 'by a deposit of fat, whilst the innermost one has a large similar pad attached to its posterior edge', and that the fin pads can be expanded into a 'cup-like surface, the use of which may be to receive the eggs as they are extruded'. Day's observations are supported by those of later authors (Rimmer and Merrick 1983: summary). Hardenberg (1935) believed that the male attaches to the female by thick hooks formed by the pad (in *Arius maculatus*) to fertilise the ova. Remarkably, although ariids form large spawning aggregations, the actual role of the thickened (and sometimes ornamented) ventral rays has elicited no scientific enquiry.

However, whereas comparatively large and few ova are produced by all ariids, not all taxa develop pads to receive them (if Day is correct). Pad-less ariids include *Sciades emphysetus, Osteogeneiosus, Hemipimelodus crassilabris, Cinetodus carinatus, Galeichthys feliceps* and *Nedystoma dayi*. Presence/absence of pads is unrelated to the maximum attainable SL of the taxon.

Possession of a padded pelvic fin in mature females is a unique ariid feature and I am bound to assign plesiomorphy to the absence of pads (following the 'commonality principle'). Nevertheless, *if* the function of the pad is to hold up the egg mass until all of it is extruded and/or fertilised (see above) the pad-less taxa could have developed some other method of supporting the ova (e.g., by extra expansion of the paired fins). The ova produced by these taxa, as far as I have been able to determine, are no smaller nor more buoyant than are those of other ariids. Nor are there differences in fecundity and maximum SL. Clearly, evidence of pad function is a prerequisite to a firm statement of polarity although I incline to the view that the loss(?) of pads is a derived feature.

State 0 = pads present in some form; 1 = pads absent.

35. *Vomer dentition.* A large, toothed vomer appears to be the primitive condition in catfishes (Bhimachar 1933; Grande 1987; Grande and Lundberg 1988). Vomerine teeth are borne on firmly attached plates or in definite patches in diplomystids, some bagrids, *Pangasius*, †*Hypsidoris*, some silurids, †*Astephus*, *Neosilurus*, clariids, schilbeids and some pimelodids (not *Rhamdia* and *Pimelodus*) and are lacking in *Synodontis* and the doradids, callichthyids and the three silurid genera in my outgroup series; also loricariids. Vomerine teeth are also present in many primitive non-ostariophysans (Fink and Fink 1981) and Ostariophysi other than catfishes (Grande and Lundberg 1988).

I concur with Bhimachar's (1933) opinion that an edentate vomer or one with very small tooth patches represents an advanced condition. Either of these conditions are found in diverse catfish groups (e.g., see above) and occur in most ictalurids (not †*Astephus*). Not infrequently, both states may occur in the one catfish family or genus, e.g., *Gephyroglanis* (Skelton 1981). There is little doubt that vomerine dentition has been lost more than once among siluroids. Within the Ariidae, the expression of teeth on the vomer is similarly highly variable although most taxa exhibit the plesiomorphic condition (Fig. 13). I have found no evidence that ariids lose their vomerine teeth with increasing age (contra Grande and Lundberg 1988).

In contrast to the above however, Chen and Lundberg (1995) stated that the plesiomorphic condition in the Amblycipitidae is of an edentate vomer and, in drawing from examples of other siluroids (including ariids), they considered that possession of teeth on the vomer in the amblycipitid genus *Xiurenbagrus* is the derived condition; and further, that possession of vomerine teeth is a homoplasy that has evolved several times in siluriform history.

State 0 = vomerine teeth present; 1 = vomerine teeth absent.

36. *Vomer dentition – stability.* As growth proceeds, the vomerine tooth patches expand slightly in some ariid taxa (the most extreme expressions being where the two oval patches coalesce and form a median patch (e.g., *Brustiarius nox*) or where one set may be lost (e.g., *Ariopsis graeffei*)).

The tendency for tooth patches to alter in shape and number during ontogeny is derived within the ariids and may be neomorphic. The phenomenon may occur in several different lineages.

State 0 = vomer tooth patch shape stable; 1 = vomer tooth patch shape unstable.

37. *Infraorbitals.* The infraorbital series in ostariophysans is primitively represented by bony, often ornamented plates (Fink and Fink 1981; Schaefer 1987). In the siluriforms, the series usually consists only of the canal-bearing portions of the bones, which are often elongate and lack ornamentation (above authors; Roberts 1973; Howes 1983). Taxa in some catfish lineages exhibit homoplasy in that the infraorbitals have expanded: e.g., loricariids, *Malapterurus* (Howes 1983), clariids (Tilak 1963b) and some doradids. In some ariids (e.g., *Batrachocephalus*) the lachrimal (first infraorbital) is expanded and peculiarly shaped.

Grande (1987) concluded that six is the primitive number of infraorbitals in siluriform fishes as it is the number common to most teleosts and also occurs in many catfish families. In contrast, Lundberg (1982) considered that the primitive number of infraorbitals is five (i.e., four plus lachrimal). In ictalurids the 'lowest and primitive' number of six occurs in two extant genera, and the fossil †*Astephus* has six (Grande and Lundberg 1988). In my outgroup material, four and five are the common numbers. *Rita* has five or six, the posterior ones being small and possibly fragmented. Two *Neosilurus* specimens have a derived count of eight: all fibrous except for the ossified lachrimal and the last enveloped by the sphenotic. Diplomystids have seven to nine (Arratia 1987) including the lachrimal. Arratia partly interpreted the high number as a derived condition, against the trend in fishes to reduce or lose infraorbitals.

The dominant number in ariids is four, including the lachrimal. The seven infraorbitals present in *Nedystoma novaeguineae* (Fig. 8) appear to be the result of fragmentation to accommodate that species' low eye. However, *Cephalocassis melanochir* has five (the second is quite small), *Bagre marinus* has six and *Bagre bagre* possibly has three. Bearing in mind the variation displayed in this character throughout the Siluriformes and the possible trend towards reduction, I interpret four (including the lachrimal) as the plesiomorphic condition in the ariids and thereby support Arratia (1987). In some ariids (e.g., *Ketengus*, *Bagre marinus*) the antero-lateral aspect of the sphenotic is produced to form a short spur which meets the last infraorbital.

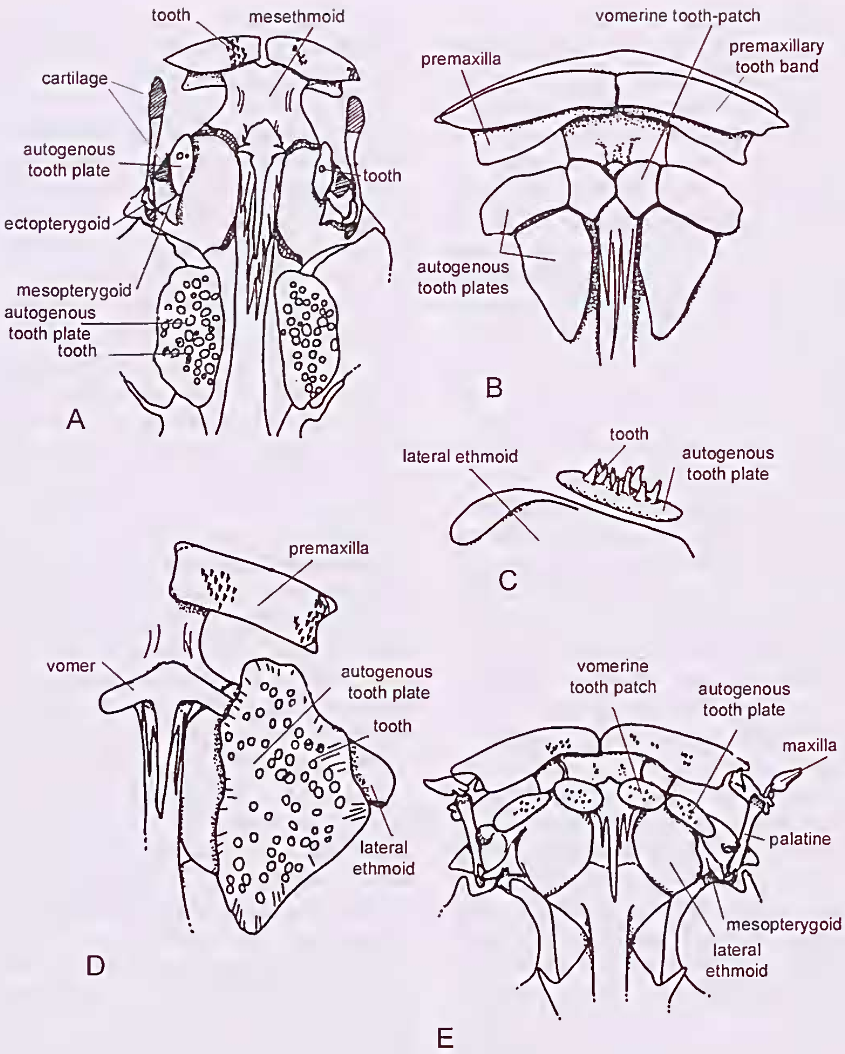

Fig. 13. Autogenous tooth plates on palate of **A**, *Plicofollis* n.gen. *argyropleuron*, 145 mm SL; **B**, *Netuma thalassinus*, 127 mm SL; **C**, *Ariopsis velutinus*, 156 mm SL; **D**, *Arius arius*, 190 mm SL; **E**, *Ariopsis utarus*, 175.5 mm SL.

State 0 = 4 infraorbitals; 1 = 5 infraorbitals; 2 = 6 infraorbitals; 3 = 7 infraorbitals; 4 = more than 7 infraorbitals.

38, 39 *Peritoneal colour; Buccopharyngeal cavity colour.* The ariids are not known for their brightness of hue, compared to the patterned body of other siluroids (e.g., auchenipterids, mochokids, loricariids). The body colour of ariids is generally uniform, although 'piebald' individuals of some taxa occur in northern Australian fresh and brackish waters. Not infrequently, colour intensity and hue vary, making a match with the colour of the surrounding water. All ariids are darker on the upper two-thirds of the body. Dark blue or brown pectoral fins are present in some taxa (e.g., *Cinetodus froggatti, Ariopsis guatemalensis, Ariopsis assimilis, Cephalocassis melanochir, Aspistor hardenbergi*). A pair of dark bands pass along the sides in *Galeichthys peruvianus*, and several taxa (e.g., *Arius maculatus, Ariopsis felis*) have dark adipose fins.

A very few ariids have a dark, dusky brown or darkly spotted peritoneum (e.g., *Hexanematichthys sagor, Arius oetik, Guiritinga barbus*). The peritoneum of *Ancharius fuscus* is brown, flecked regularly with cream. Just as few others (e.g., *Aspistor platypogon, Brustiarius nox*) have a dark buccopharyngeal cavity, the colour extending over the gill rakers.

The expression of definite colour in the ariids appears to be sporadic. In an attempt to determine whether it reflects synapomorphies in a phylogenetic relationship or was independently derived within the family, peritoneal colour and buccopharyngeal colour were scored for analysis. Any selective 'advantage' taxa may achieve through having definite colours has not been investigated.

Peritoneal colour. State 0 = dark peritoneum; 1 = pale or slightly dusky peritoneum.

Buccopharyngeal cavity colour. State 0 = dark cavity; 1 = pale cavity.

40. *Secondary hypurapophysis.* The 'Type C' hypurapophyses of Lundberg and Baskin (1969), of combined hypurapophyses and secondary hypurapophysis extending over the parhypural and first two hypurals, is an advanced character state among catfishes. This condition is exhibited by all ariids although some minor variations are apparent.

A more derived secondary hypurapophysis condition is exhibited in some ariids such as *Arius argyropleuron*, in which the structure is flattened and 'teardrop'-shaped.

State 0 = secondary hypurapophysis flattened and 'teardrop'-shaped; 1 = not as above.

41. *Size of the caudal vertebrae.* Ariids exhibit some interspecific variation in size and form of the vertebrae. The enlarged anterior caudal centra in the marine ariid *Netuma thalassinus* are twice as wide as centra in other parts of the column (Kailola 1986). In *Aspistor quadriscutis*, the posterior caudal centra are considerably elongated, and in *Bagre marinus* they appear to be vertically extended.

Although objective comparison between forms proved unreliable in the cleared and stained material I examined, the size ratio between the tenth penultimate vertebral centrum and the penultimate vertebral centrum was used to quantify observed size differences. Whereas in most other ariids the penultimate vertebral centrum is 10–40% narrower than the tenth penultimate centrum, in *Plicofollis* n. gen. *argyropleuron* the distal caudal vertebrae are shortened and extend vertically such that the last centra are at least half the width of the tenth penultimate centrum.

State 0 = last caudal centra much narrower than other centra; 1 = no great disparity in size of vertebral centra with tenth penultimate centrum up to 40% wider than remaining centra; 2 = anterior caudal centra twice wider than remaining centra.

42. *Size of nuchal plate.* In the majority of siluroids, the nuchal ('predorsal') plate is a narrow crescentic bone at the proximal base of the first dorsal spine or buckler and it forms a rigid supporting connection between the skull and the dorsal fin elements. However, in some ariids the nuchal plate is enlarged, a character state also present in some pimelodids (Lundberg *et al.* 1988). Although Taylor and Menezes (1977) considered that the nuchal plate is enlarged at all growth stadia in these ariid groups, this is not so. In some *Sciades* and *Aspistor* species, *Hexanematichthys sagor* and *H. mastersi* the nuchal plate expands during ontogeny.

State 0 = relative size of nuchal plate increasing with growth; 1 = relative size of nuchal plate not changing with growth.

43. *Rakers on posterior edge of the gill arches.* Members of the Ariidae either have or lack gill rakers on the posterior faces of the first two gill arches (Taylor 1964; 1986; Roberts 1978; Kailola 1983). Sometimes the rakers are confined to the dorsal-most part of the arches, sometimes they are lacking from the first arch but present on the second arch, and sometimes they are 'club'-shaped and arranged into two rows (in some *Cathorops* species). They may be short (e.g., *Ketengus*) or very long (e.g., *Osteogeneiosus*).

Presence of posterior rakers on all four gill arches was considered plesiomorphic by Stewart (1986) because rakers are present in this situation in the primitive family Diplomystidae. Many of the outgroup taxa have such rakers. Skelton (1981) observed that the character is difficult to evaluate and appears to have a complex distribution within the Siluriformes, likely associated with functional demand.

State 0 = rakers present on posterior face of all arches; 1 = rakers absent from posterior face of first arch; 2 = rakers absent from posterior face of first and second arches.

44. *Pelvic fin elements and pelvic musculature.* All ariids have six segmented rays in the pelvic fin (in the outgroup material, the number of fin elements decreases from 11–13 in *Neosilurus* and *Parasilurus* and nine in *Ompok* and *Pylodictus,* to five in the loricariids (see also Grande 1987)). According to Lundberg (1970, cited in Grande 1987) and Grande (1987), primitively there are six segmented rays in the catfish pelvic fin. In conjunction with the low ray count, ariids have a very complex and highly specialised pelvic musculature, described by Shelden (1937). These muscles have a powerful grasping function consistent with the development and possible function of ariid secondary sex characteristics. Moreover, this complex musculature is not lacking from males and taxa in which maturing females do not develop pelvic fin pads (see Character 34). Albeit a low (and primitive) segmented ray number, the combination of ray number with the complex pelvic muscle form and basipterygium shape (Shelden 1937) is derived for the Ariidae.

State 0 = 6 elements + specialised pelvic musculature; 1 = 7 elements, no homologous musculature; 2 = 8, ditto; 3 = 11–13, ditto; 4 = 9, ditto; 5 = 5, ditto.

45. *Caudal elements.* Lundberg and Baskin (1969) determined that the number of principal caudal fin rays is constant within catfish taxa having forked tails (e.g., the Ariidae). The most primitive caudal ray count of 9+9 occurs in the Diplomystidae within the Siluriformes, and ostariophysans and primitive teleosts have 10+9 rays (Lundberg and Baskin 1969; Arratia 1987). †*Hypsidoris* and the majority of siluroids have 17 (8+9) principal

caudal rays (Lundberg and Baskin 1969; Grande 1987; Grande and de Pinna 1998). The ariids have a derived count of 7+8; only loricariids, amphiliids, aspredinids and some akysids (e.g., *Breitensteinia* Steindachner) having a lower regular count.

State 0 = 7+8; 1 = 8+9; 2 = 7+7; 3 = 8+8; 4 = 9+9; 5 = variable (e.g., *Neosilurus*).

46. *Presence and length of posterior dorsomedian fontanelle.* In †*Hypsidoris* the dorsomedian fontanelle is long, extending behind the supraoccipital-frontal articulation at all growth stadia. In siluroids there is a trend towards closure. Howes (1985) considered that absence of a posterior cranial fontanelle is a common phenomenon in siluroids and thought that the condition could be derived; but if so, it must have developed independently in several lineages. Accordingly, the presence of a well-developed posterior fontanelle extending to, just short of, or beyond the supraoccipital-frontal articulation and remaining open in adults, appears to be the plesiomorphic condition.

The Ariidae is one of the siluroid families which exhibits the trend towards closure. In ariids, the double dorsomedian fontanelle in juveniles usually extends from the mesethmoid to the region of the supraoccipital-frontal articulation (Fig. 14). The posterior fontanelle tends to reduce or be absent in adults yet may remain moderately large in some taxa.

State 0 = fontanelle very small or absent (even in juveniles); 1 = fontanelle reducing during ontogeny; 2 = extensive fontanelle, always open.

47. *Shape of posterior dorsomedian fontanelle.* An elongate-rectangular posterior fontanelle of most catfishes appears to be the plesiomorphic condition (see also Tilak 1963, 1964, 1965a; Lundberg 1982; Arratia 1987; Grande 1987). An irregularly-shaped or rounded posterior fontanelle therefore represents the derived condition – as in the Ictaluridae (Lundberg 1982) and Auchenipteridae (Curran 1989). The bagrid *Chrysichthys* and several ariids have a small, heart-shaped posterior fontanelle (including *Hemiarius stormii, Nedystoma dayi, Ariopsis robertsi* and *Cephalocassis melanochir*) and irregularly-shaped fontanelles occur in *Amissidens* n. gen. *hainesi* and *Nemapteryx armiger*. Curran (1989) considered that a fontanel with unique convoluted edge is derived.

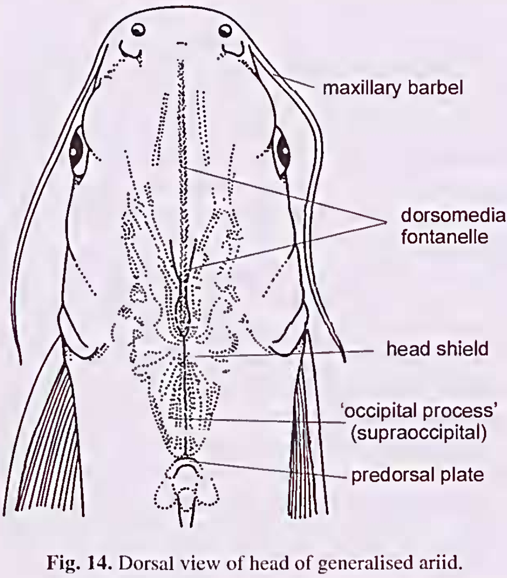

Fig. 14. Dorsal view of head of generalised ariid.

State 0 = elongate-rectangular fontanelle; 1 = rounded or ovate-triangular fontanelle.

48. *Size of the frontals.* In *Arius arius* the frontal is moderately elongate and bifurcates anteriorly; in some other ariids (e.g., *Netuma bilineatus, Bagre*) it is much expanded anteriorly in older individuals, dorsally overlapping its arms; while in other taxa the frontal is rectangular and/or narrow with long arms.

The forward spread of the frontals is influenced by growth in some ariids. For example, the space between the lateral ethmoid and frontals is considerably reduced or absent in larger individuals of *Hexanematichthys sagor, Sciades proops, S. parkeri, Aspistor kessleri* and *Bagre marinus*. I consider that two derived character states exist: i) broad anteriorly and tapered to moderate or narrow posteriorly, arms wide and frontal-lateral ethmoid space reduced; and ii) broad posteriorly with tapered, narrow arms anteriorly and often a large frontal-lateral ethmoid space (e.g., *Cathorops, Nedystoma dayi, Nemapteryx armiger*).

State 0 = frontal broad anteriorly and moderately narrow posteriorly, anterior space reduced (adults) and arms moderately wide; 1 = frontal moderately broad posteriorly, anterior space moderately enlarged; 2 = frontal broad posteriorly, anterior arms narrow, space enlarged.

49. *Laminar bone over the anterior vertebrae.* The laminar bone is usually continuous medianly in ariids (except in *Galeichthys* and *Ancharius*) and is more extensive in larger individuals, an ontogenetic change evidenced in most taxa. However, the excavation of the laminar bone posteromedially and the overlapping of the transverse process bases laterally is variable. I consider that a minimal cover over the aortic groove is plesiomorphic in ariids and interpret a 'minimal cover' as exposed transverse process bases and a deep median excavation on the ventral surface. The laminar bone in ariids extends over four to eight vertebra centra. Some ariids possess apomorphic modifications in the laminar shelf, such as depressions (e.g., *Guiritinga barbus, Cinetodus froggatti*) or median single keel (e.g., high and acute in *Batrachocephalus, Nemapteryx armiger*) or double keel (e.g., *Bagre marinus*).

The laminar bone in other siluroids extends laterally over the first four to six vertebrae to a greater or lesser degree. The laminar bone extensively overlaps the bases of the vertebral transverse processes in the four bagrid taxa (not *Rita*) and *Pimelodus* that I examined.

State 0 = deeply excavated medially, 4th–6th transverse process bases largely exposed or expanded; 1 = moderately excavated medially, 4th–6th process bases moderately to well covered; 2 = shallow excavation medially, 4th–6th process bases concealed; 3 = convex or truncate posterior margin.

50. *Additional palate dentition.* The teeth often present on the siluroid palate are borne on autogenous tooth plates. Examples of catfishes bearing such plates are †*Hypsidoris*, †*Astephus*, some bagrids (Tilak 1965; Skelton 1981; Bailey and Stewart 1984; pers. obs.); *Schilbe, Pangasius, Ompok* (pers. obs.), other silurids (Bornbusch 1995), several pimelodids (Schultz 1944; Mees 1974; Grande and Lundberg 1988) and ariids. Fink and Fink (1981) regarded the presence of tooth plates as neomorphic because they are also present in some groups of characiforms (see also Gosline 1975) and Roberts (1973) implied that tooth bearing plates arose independently in characins and catfishes. A good summary of information on autogenous tooth plates and description of their fickle nature in the silurid *Hito* is given by Bornbusch (1995). I consider the possession of autogenous palatal tooth plates as plesiomorphic in the Ariidae. When present, the tooth plates are either ovate, elongate-oval, roughly triangular or triangular with concavities posteriorly.

However, the presence of fixed tooth plates on the parasphenoid and/or orbitosphenoid in *Sciades* and *Aspistor* (and rarely in other ariid individuals) is an apomorphy, possibly secondarily derived within fishes (see Gosline 1971). Similar, independent apomorphies have been recorded elsewhere: fixed toothed plates in a schilbeid (Tilak 1961); tooth plates below or attached to the palatine in diplomystids (Arratia 1987; Azpelicueta 1988); and in *Chrysichthys* (Mo 1988).

State 0 = autogenous tooth plates always present; 1 = autogenous tooth plates absent.

51. *Position of palatal tooth plates.* The form and position of the autogenous tooth plates (Fig. 13), constant within an ariid taxon, have been used almost solely as defining characters in taxonomic works on the family (e.g., by Günther 1864; Day 1877; Weber and de Beaufort 1913). There may be one plate on each side of the palate anteriorly, adjacent to the vomer tooth patch (or edentate vomer) and lying ventral to the anterolateral aspect of the lateral ethmoid or more posteriorly over the metapterygoid on each side (as in *Arius arius*); or the plates may be paired, forming a toothed triangle with the vomerine teeth (as in *Netuma thalassinus*); or even of longitudinally arranged anterior small and posterior larger patches, the latter extending as far back as the hyomandibular. In some taxa, the palatal dentition is 'broken' into several patches on each side (e.g., *Genidens genidens, Netuma planifrons*, cf. *Arius harmandi*). Further, individuals rarely may develop additional autogenous tooth plates, a phenomenon I have observed in *Plicofollis* n. gen. *nella* and *Arius dispar*.

I consider the anterior plate position as plesiomorphic in ariids.

State 0 = tooth plates at front of palate or anterolaterally; 1 = tooth plates longitudinally arranged: small anterior patch, larger elongate posterior patch.

52. *Dentition on palate tooth plates.* The form of palate dentition in ariids is probably associated with feeding specialisations (see also Gosline 1975): fine and villiform, conical, acute, small and curved, 'peg'-like and molariform. Where palate teeth of ariid taxa are granular or globular, they are noticeably larger than the jaw teeth (except in *Cathorops* in which granular teeth are often present in the lower jaw band) but, apart from the presence of sea urchins (echinoderms) in the gut of juvenile *Plicofollis* n. gen. *nella* (pers. obs.) and *Arius tenuispinis* (= *Plicofollis* n. gen. *layardi* jun. syn.; Al-Hassan *et al.* 1988), very little information on the diet of such taxa is available. A character not compared in my analysis was form of the palate dentition, as I considered (erroneously perhaps) that its expression was related only to diet and thus imparted little phylogenetic information. Clearly, palate dentition in the Ariidae falls into the two general groups; of fine, conical, acute, small, and 'peg'-like, molariform, granular.

Nonetheless, the presence or absence of teeth on the tooth plates appears to be a useful phylogenetic character as tooth presence is variable in ariids and independent of diet. The usual condition is for teeth to be present on the palatal tooth plates in catfishes, but in *Amissidens* n. gen. *hainesi*, the tooth plates are never toothed and in *Ariopsis velutinus*, normally untoothed plates occasionally bear teeth. Interestingly, the males of some ariid taxa having granular palatal dentition (e.g., *Arius maculatus, Plicofollis* n. gen. *nella*) shed many teeth during the spawning (= brooding) period (Day 1977; Willey 1911; pers. obs.). Individuals of *Brustiarius solidus* of various sizes, maturity and either sex also shed teeth, the cause of which is undetermined.

State 0 = plates always toothed; 1 = plates always untoothed; 2 = plates occasionally lacking most teeth.

53. *Fin spine thickness.* The presumed plesiomorphic condition of the fin spine in catfishes is of a well-ossified spine with strong and/or few well-developed, retrorse serrations along the posterior and often distal anterior margin(s). This condition occurs in many siluroids. According to most authors, the derived form of the fin spine in catfishes is of a moderately slender spine, often flexible, and with serrations only along the posterior margin. Stewart (1985, 1986, 1986a), Lundberg and McDade (1986), Buckup (1988) and Ferraris Jr (1988) discussed the phylogenetic implications of this apomorphy in the Pimelodidae. Loss of spines altogether and absence of a dorsal fin (Fink and Fink 1981; Howes 1985) appear to be related apomorphies.

The Ariidae display interspecific variability in spine thickness and serrature and spines often thicken with age. Spines may be hard and stout with strong serrae or dentae, thin and finely serrated, distinctly rugose (e.g., *Nemapteryx nenga*), flat and broad, or formed by peculiar diagonal layering of supporting tissue (pectoral spine, *Bagre marinus*). As with skull ornamentation (character 28) however, I am not decided on whether the derived condition is only that of a thin, finely serrated spine. The impressive ornamentation of spines in taxa such as *Nemapteryx macronotacanthus*, and the array of large serrations (dentae) along the inner margin of the pectoral spine in taxa such as *Cinetodus carinatus, Ariopsis assimilis, Aspistor luniscutis* and *Nedystoma novaeguineae* suggest that such character states are also derived. An additional (unrelated) apomorphy displayed by some taxa (e.g., *Cephalocassis borneensis*, *Aspistor platypogon* and *Cryptarius* n. gen. *truncatus*) is a series of low ridges along the inner pelvic fin rays.

State 0 = spines robust, moderately thick and strong; well-serrated; spine thickness increases with growth; 1 = spines very thick, may be very rugose (sometimes internally chambered) and/or flattened or broad; 2 = spines moderately thin, but with strong serrae; 3 = spines moderately thin with fine serrae; 4 = very thin with few low serrae and somewhat flexible.

54. *Branchiostegal number.* There is considerable variation in number of branchiostegals in catfishes and the plesiomorphic combination of higher number of branchiostegals, extensive gill opening and broad membrane is exhibited in many taxa. McAllister (1968) and Grande (1987) compared 18 catfish families and found that the more phylogenetically derived families possess fewer branchiostegals. Overall, the numbers range from 20 (Siluridae) to three (Callichthyidae). Some authors (e.g., Alexander 1965; Lundberg 1982) believed that a higher number is associated with a flattened head in catfishes; but Gosline (1973) doubted there is any correlation with head shape. He argued that the branchiostegal number is related to the tightness-of-fit of the gill cover over the gill chamber during inspiration and that the number of rays (or struts) is positively associated with the length of the gill cover's anteroventral portion (more to fan out over a larger area, fewer to cover a smaller area). Gosline (1967) found there is often a three-way relationship between fewer branchiostegal rays, a broadly-united gill membrane and shorter lower jaw.

The Ariidae have *fewer* branchiostegals than do other catfishes having gill openings of comparable size and so appear to be apomorphic in this character. Even so, within the family it is difficult to suggest a trend for this character. Whilst most ariids (with either wide or restricted gill openings) have six branchiostegals, a few have seven: e.g., *Hemiarius stormii, H. dioctes, Arius platystomus* (Tilak 1965); and others having five have either a restricted (e.g., *Batrachocephalus mino*) or wide gill opening (e.g., *Netuma thalassinus*).

In all ariids, the first two (outer) branchiostegals are broader than are the remainder and they may act as a suboperculum (a bone lacking in this family) (Tilak 1965; Lenous 1967; Gosline 1973). The first ray in some taxa (e.g., *Plicofollis* n. gen. *argyropleuron, Cathorops, Ketengus*) is exceptionally broad, an apomorphy probably independently derived within the Ariidae.

State 0 = 4 branchiostegals; 1 = 5 branchiostegals; 2 = 6 branchiostegals; 3 = 7 branchiostegals; 4 = 8–9 branchiostegals; 5 = more than 9 branchiostegals.

55. *Abdominal/precaudal vertebrae ratio.* There is considerable variation in the length of the abdominal cavity in Siluriformes and Lundberg and Mago-Leccia (1986) discussed the direction of change of this character which may be associated with the relative size of the swim bladder. Albeit I found no clear correlation between swim bladder size and cavity length in ariids I examined, it is possible that there is one.

Sensu Lundberg and Mago-Leccia (1986) I determined the cavity length indirectly by calculating what percentage of the vertebral column was comprised of precaudal vertebrae (i.e. fused vertebrae of the anterior complex plus those with an open haemal arch), assuming all vertebral centra are of equal size. In the ariids, the number of precaudal vertebrae ranges from 12 in *Arius quadriscutis* to 30 in *Leptarius dowii*. The range in percentage of the vertebral column of all catfishes I examined is 24 (*Aspistor kessleri, A. luniscutis, A. quadriscutis*) to 47 (*Sciades proops, Plicofollis* n. gen. *nella*). In other catfishes, the number of precaudal vertebrae ranges from nine (*Hypostomus*) to more than 19 (*Pterodoras*, diplomystids, some ictalurids and *Clarias*). In †*Hypsidoris oregonensis* Grande and de Pinna (1998) there are 18–19 precaudal vertebrae.

State 0 = precaudal vertebrae 39% or more of total vertebral number; 1 = precaudal vertebrae 33–38% of total vertebral number; 2 = precaudal vertebrae 32% or less of total vertebral number.

56. *Naked body.* A scaleless body is a derived condition in the ostariophysans. Most cypriniforms, characiforms and most primitive teleosts and gonorhynchiforms possess scales on all or part of the body, while the majority of catfishes (including ariids) and gymnotoids lack scales – although scales are often represented by ossified lateral line tubes (Roberts 1973; Fink and Fink 1981). Some catfishes (doradids, loricariids) possess bony plates or toothed scutes on the body. However, it is possible that such 'armature' is not homologous with the body scales of other ostariophysans (Roberts 1973; Fink and Fink 1981).

State 0 = possession of bony plates or toothed scutes on the body; 1 = naked body.

57. *Gonad reduction.* Most female ariids possess paired gonads of an unlobed, hollow type (Rimmer and

Merrick 1983). The exceptions are *Nedystoma dayi* and *N. novaeguineae*. In these taxa, the gonad forms a single, ovate unit having an internal incomplete septum. In *Amissidens* n. gen. *hainesi* and *Cryptarius* n. gen. *truncatus*, the proximal third of the ovaries are united.

In these oral incubating fishes, the number of mature ova produced at each spawning is directly related to the number that can be accommodated in the male parent's mouth: i.e., the smaller the parent, the less capacity has his mouth. Production and fertilisation of more ova than can be viably accommodated might be interpreted as a 'waste' of reproductive effort. One solution could be to produce more *smaller* ova, but for fishes hatching large, precocial larvae (Fuiman 1984) as do the ariids, there must be a minimum amount of yolk required in the ovum. The alternative, of reducing the gonadal epithelium such that *fewer* ova are produced, appears to be the *modus operandi* in these small ariids (maximum recorded SL of *Nedystoma dayi* is 300 mm SL, of *Nedystoma novaeguineae*, 150 mm SL). Welcomme (1967) reported a similar relationship in the mouthbrooding *Tilapia* (Cichlidae), where the number of ova produced approximately equals the square of the total length (cm) of the parent fish. However, this 'argument' may not hold good, as *Amissidens* n. gen. *hainesi* attains 320 mm fork length, and *Cryptarius* n. gen. *truncatus* attains 420 mm total length – maxima certainly not among the smallest in the Ariidae.

State 0 = reduced gonad shape; 1 = gonad 'normal' shape, bilobed.

Characters not used in the analysis.

1. *Equivocal, stable or problematic characters.*

Pectoral girdle. Howes (1985) observed that a rigid girdle is lacking in midwater, shoaling fish (but see *Bagre marinus*, below), while loricariid catfish, which live on the substrate, have a reinforced girdle (Schaefer 1984).

In the ariids, the cleithrum and coracoid are broadly united for most of their lengths. At the midline, the coracoids and part of the cleithrum are joined by 5–12 pairs of interdigitations, such a joint providing strength and rigidity to the girdle (Roberts 1973). A complete/broad midline connection between the coracoids is widespread and probably plesiomorphic in catfishes (Howes 1985; Bornbusch 1995). *Schilbe, Synodontis, Pimelodus*, the doradids and some bagrids have extensive girdle shelves, a feature lacking in the more derived Siluridae and Helogenidae (Alexander 1965). However, the derived ictalurid *Trogloglanis* has a broad symphysis compared to that in confamilials (Lundberg 1982) and *Bagre marinus* has a broad and strong shelf. In *Cathorops*, the cleithrum is ridged and expanded laterally. Probably a broad pectoral symphysis is apomorphic in ariids.

In ariids, the pectoral girdle curvature varies from being shallow and/or thin (e.g., in *Brustiarius nox, Cochlefelis danielsi*) to strong, stout and compact (e.g., in *Cinetodus froggatti*, cf. *Arius macrorhynchus*). The coracoid keel is strong, high and clearly defined in some taxa (e.g., *Cathorops, Arius manillensis*) and low and flat in others (e.g., *Cephalocassis melanochir*). Although marked differences could be recognised, differences in height of the coracoid keel and coronoid process and amount of curvature of the girdle between different taxa could not be quantified because of ontogenetic variation and fallible measurement of curvature. The coronoid process height is significant in †*Hypsidoris* (Grande 1987), while a short keel is plesiomorphic in ictalurids (Lundberg 1982).

Caudal skeleton. In ariids, the caudal skeleton consists of: parhypural; hypural 1+2; hypural 3+4; hypural 5; epural. In much of the skeletal material examined (of smaller individuals) the hypurals were imperfectly ossified and sometimes the third and fourth hypurals are incompletely fused. The significance of the trend for caudal elements to unite or ossify as growth proceeds could not be assessed here because of differences in the SL of the examined material, yet the parhypural is clearly sutured with hypural 1+2 in, for example, *Plicofollis* n. gen. *nella, Netuma thalassinus* and *Cinetodus crassilabris* and partially fused with hypural 1+2 in *Galeichthys*. Lundberg and Baskin (1969) recorded variation in element fusion in different-sized ariids (including unfused in a 400 mm SL specimen of *Potamarius*!).

I was also unable to adequately quantify the limited variation exhibited in the size and position of the epural. Lundberg and Baskin (1969) and Arratia *et al.* (1978) noted a trend towards loss of this element in the Trichomycteridae, and it is specifically polymorphic in the Pygidiinae (Arratia 1983).

Hyomandibular articular facet. This facet either lies on the sphenotic (e.g., *Arius manillensis*), or extends over the sphenotic-pterotic suture (e.g., *Aspistor kessleri*) or occasionally (e.g., *Aspistor hardenbergi, Plicofollis* n. gen. *nella, Sciades troschelii*) it reaches as far as the front of the pterotic, a condition shared with other siluroids such as the Bagridae, Schilbeidae and Pimelodidae. This character's significance in the ariids could not be accurately assessed from the material examined.

Fifth parapophyses. In most ariids the parapophyses emanating from the anterior vertebrae are directed posterolaterally. However, in *Nedystoma dayi, Hemiarius insidiator, Osteogeneiosus* and *Genidens* they are directed at right angles to the vertebral centra. This condition also exists in the Ictaluridae (Lundberg 1982). In *Cathorops* and *Potamarius* the fifth parapophyses is angled forward or directed outwards, and may be united with the sixth (in a peculiar shape: *Potamarius*). The significance of these character states was not investigated.

Pelvic girdle. Shelden (1937) suggested that absence of a posterior process to the basipterygium is plesiomorphic in catfishes, and Grande (1987) pointed to the correlation between lack of a process and higher number of pelvic fin rays (more than seven) in about six catfish families. The form of the pelvic girdle posteriorly only varies slightly in most ariids (Tilak 1967a) and the basipterygium is generally short; but in *Cathorops* the basipterygium has an extensive, rounded posterior process, in *Bagre marinus* the posterior process is perhaps more extensive but with a truncate termination, and in *Potamarius* it is enlarged and rounded.

Urohyal shape. A triangular urohyal (when viewed from below) is common in catfishes, although considerable variation in this character is displayed throughout the Siluriformes. In some groups the urohyal is slender (e.g., the Schilbeidae, some bagrids, some silurids and the pimelodid *Rhamdia*), while in others it is broad and triangular (e.g., the bagrid *Gephyroglanis* (Skelton 1981), the ictalurid *Trogloglanis* (Lundberg 1982), *Pimelodus* and the loricariid *Hypostomus* (Schaefer 1987) and the Chacidae (Brown and Ferraris Jr 1988)). In diplomystids the urohyal has short anterior processes and a long, median posterior extension (Arratia 1987), and in †*Hypsidoris* and †*Astephus* it has three well-defined processes directed ventrally (Grande and Lundberg 1988; Grande and de Pinna 1998).

The urohyal in the Ariidae is often narrow, the posteromedian and lateral arms long and tapered. In some (e.g., *Cathorops*) it is broad and anteriorly truncate; in *Brustiarius nox, B. solidus* and *Nedystoma novaeguineae* the lateral arms are very slender and tending to bifurcate distally; in *Galeichthys* and *Aspistor kessleri* it is concave anteriorly and broad posteriorly; and in *Cephalocassis borneensis* the arms are broad. Although Lundberg (1982) suggested that a narrow urohyal is more primitive in catfishes, my findings in the Ariidae do not endorse this. Unfortunately, the character states of the ariid urohyal are difficult to define unequivocally, and there is intraspecific and ontogenetic variation in some taxa.

Otoliths. When fresh material was available, the lapillus otolith (Arratia 1987) was extracted from the utriculus region of the skull and examined in an attempt to recognise and compare interspecific variation in form. The otolith shape is extremely uniform in the ariids and I found no assessable changes, except those associated with growth. However, when comparing the relative *weights* of otoliths taken from specimens of *Ariopsis midgleyi* and *A. graeffei* from Lake Argyle, northwestern Australia (Kailola and Pierce 1987), and miscellaneous collections of Sahul Shelf ariids, I found considerable interspecific variation.

Weberian apparatus. Features of the Weberian apparatus are useful in classifying the families of catfishes, but of limited use for finer resolution (Chardon 1968; Fink and Fink 1981). Krumholz (1943) found that ossicles differed in form between various North American ostariophysans; and Tilak (1965) attempted to show they do in ariids. Chardon (1968) perceived some variability in the shape of the ossicles in catfishes but attributed the variation to skeletal strength and other general adaptations. I also found no substantial differences in these structures in ariids; and as they are very small and easily damaged when extracting, I consider that any perceived differences in their form cannot be reliably used to distinguish between taxa.

Axillary pore. The pore (of the axillary gland) is located just ventral to the posterior cleithral process in most catfishes. In *Diplomystes chilensis* the opening is rounded or elongate, most individuals having two openings in each axil (Arratia 1987). Lundberg (1982) observed that the pore size is variable in the Ictaluridae, frequently lost with growth and absent in the derived genus *Trogloglanis*. Generally in ariids, the opening is moderately small. In *Cinetodus*, *Potamarius* and *Aspistor luardenbergi* however, the opening is enlarged and ovate, while in other taxa (e.g., *Plicofollis* n. gen. *dussumieri, Brustiarius solidus, B. nox*) it is tiny. My attempts to quantify pore size proved unreliable, particularly on preserved material.

Ascending parasphenoid alary processes ('wings'). Alary processes are present in most catfishes (Bhimachar 1933): they suture with the pterosphenoid and thereby separate the optic foramen anteriorly from the trigeminofacial foramen. *Diplomystes* lacks the bony 'wings', as do *Trogloglanis* and some trichomycterids (Lundberg 1982). The alary processes are frequently well developed in ariids and they range in shape from slender, long spurs (e.g., in *Aspistor kessleri, A. luniscutis, Nemapteryx augustus,* cf. *Arius rugispinis*), to groups of spurs (e.g., *Ariopsis felis*) to broad, low flanges (e.g., in *Nedystoma dayi, Arius manillensis*), to no process (*Potamarius*). In *Bagre marinus* the spur is so long it lies dorsad to the metapterygoid! The alary processes are often fragile however, and the considerable intraspecific and ontogenetic variation in their shape (and presence) precluded their meaningful contribution to a phylogenetic analysis.

Ossification. The well-ossified neurocranium of diplomystids and many other siluroids appears to be plesiomorphic, yet according to Bhimachar (1933) a superficially bony skull is apomorphic among catfishes, just as is a thinly-ossified skull. Thinning of the skull bones and/or presence of persistent cartilage in adults is a derived condition often apparent in taxa achieving a small maximum size (Lundberg 1982). The ictalurid situation is mirrored in the Ariidae: weak cranial ossification occurs in *Nedystoma novaeguineae*, *Bagre*, *Cephalocassis borneensis* and *C. melanochir*, and there is a tendency towards it in *Brustiarius nox* – all of these are taxa attaining a small maximum size. Cartilage persists in adult stadia between the sphenotic, pterotic and supraoccipital in *C. borneensis* and *C. melanochir*. Other ariids (e.g., *Cinetodus carinatus, Batrachocephalus, Osteogeneiosus*) display a second apomorphy: a heavily ossified skull, especially posteriorly. Howes (1983) and Stewart (1986) described poorly ossified cranial bones of some pimelodids as 'honeycomb texture with the frontal papyraceous' or 'appearing extremely porous', and such phenomena occur in, for example, *Bagre* species (frontal bones), *Plicofollis* n. gen. *dussumieri, Plicofollis* n. gen. *nella* and *Osteogeneiosus* (lateral ethmoid expansion), *P.* n. gen. *nella* again (expanded supraoccipital process) and *Sciades* species (nuchal plate).

Relative skull ossification is, however, difficult to qualify; and more than one character seems to be involved.

Premaxillary thickness. This character was difficult to qualify. Although the premaxillary is usually well-ossified in ariids, it is reduced and thin in some taxa, a condition I consider derived. Examples of taxa having a thin premaxillary are *Nedystoma dayi* and *Amissidens* n. gen. *hainesi*. In contrast, the premaxillaries of *Batrachocephalus* and *Ketengus* are very extensive and strongly ossified. Lundberg (1982) and Stewart and Pavlik (1985) cited similar situations in the ictalurid *Trogloglanis* and the pimelodid *Cheirocerus*. A possibly homoplastic condition exists in the gonorhynchiforms which have very thin and flat premaxillaries (Fink and Fink 1981).

Lateral ethmoid shape. The usual and presumed plesiomorphic condition of the lateral ethmoid is short and triangular to rhombic (e.g., Fink and Fink 1981; Howes 1983, 1983a). In some ariids (e.g., *Plicofollis* n. gen. *argyropleuron, P.* n. gen. *nella*) the prominent 'eyebrow' of large individuals is a good distinguishing feature. In the Ariidae there are several states of the outer, lateral prominence ('wing') of the lateral ethmoid, suggesting trends or synapomorphies in the family. About five different shapes occur in the ariids: triangular and/or rhombic (*Bagre marinus, Hemiarius grandicassis, Galeichthys*), or almost square/rectangular (*Ariopsis felis, Nedystoma dayi*), through sharp and attenuated (*Plicofollis* n. gen. *layardi, P.* n. gen. *argyropleuron, Brustiarius nox*), shallow and curved posteriorly (*Nedystoma novaeguineae*), long, slender and acute (*Arius manillensis, A. dispar*) to large, truncate and oblong, expanded, and posteriorly directed (e.g., *Plicofollis* n. gen. *polystaphylodon, P.* n. gen. *dussumieri, Hemiarius grandicassis, Potamarius*). The lateral ethmoid is extensive ventrally in, for example, *Cochlefelis spatula, C. danielsi, Netuma bilineatus* and *Aspistor kessleri* and obscures the space between the frontal arms.

The influence of ontogeny and intraspecific variation in the shape of the lateral ethmoid could not be assessed, and also, clear qualitative description proved difficult. This character may impart significant phylogenetic information; for example, Bornbusch (1995) used lateral ethmoid shape in his phylogenetic analysis of the Siluridae, and Armbruster (1998) used the character in analysing loricariids.

Palatine facet. In summarising the different forms of the siluroid palatine, Howes (1985) found that on 'grounds of commonality' the bone is rod-shaped and articulating with part of, or the entire, lateral ethmoid margin. This is the situation in the Ariidae, in which the articular facet lies half to two-thirds along the length of the palatine.

The extent of the palatine-lateral ethmoid contact differs among the ariids: a long facet (e.g., as in *Plicofollis* n. gen. *nella*) appears to be the derived character state. Whereas de Pinna and Vari (1995) found the length and position of the palatine facet diagnostic for the Cetopsinae, I was unable to reliably quantify facet length in much of my material. Furthermore, although a short palatine appears to be derived, relative *palatine length* is difficult to assess, although it appears to differ among ariids.

Supraoccipital shape. The majority of siluroid taxa possess a triangular, flat supraoccipital bone which is tapered posteriorly to meet the nuchal plate (or preceding supraneural) before the dorsal fin. This apparently plesiomorphic system lends support to the dorsal spine-locking mechanism of some groups (Lundberg 1982) such as *Pangasius* (Tilak 1964), †*Hypsidoris* (Grande 1987) and most ariids. The ariids display about three derivations of the primitive supraoccipital form, although the effect of ontogeny appears to be significant. The posterior section may be slender and rectangular (as in *Galeichthys, Hemiarius insidiator, Cephalocassis*); or very broad, often short (as in *Aspistor hardenbergi, Sciades, Hexanematichthys sagor*). The slender process in *Plicofollis* n. gen. *nella* and *Hemiarius grandicassis* (and some other taxa) expands outwards as growth proceeds.

This character could have contributed to the phylogenetic reconstruction. It was omitted because of anticipated high levels of homoplasy and uncertainty whether character states could be accurately recognised in the different taxa (e.g., because of overlapping muscle tissue). Another related character, the height and form of the medial longitudinal keel on the supraoccipital in some taxa, could not be adequately quantified. The keel is frequently more dominant in juveniles.

Uncinate process, epibranchial 3. As in the Diplomystidae (Arratia 1987), only the third epibranchial bears an uncinate process in the Ariidae. This apomorphy is shared with several Asian catfish families (Tilak 1963; 1963b; 1964; pers. obs.), the Bagridae (Tilak 1965a; Skelton 1981; pers. obs.), Chacidae (Brown and Ferraris Jr 1988), Plotosidae and Doradidae.

Although Mahajan (1966) believed that possession and form of the uncinate process was 'significant' in catfishes, unequivocal recognition of the various character states proved difficult in the material I examined. In most Ariidae, the uncinate process is angular and overlaps the middle of the fourth epibranchial, a condition I consider plesiomorphic. In some taxa (e.g., *Plicofollis* n. gen. *argyropleuron*) it is expanded slightly; in *Hemiarius insidiator* it overlaps the proximal part of the fourth epibranchial; and in *Brustiarius nox* and *B. solidus* the process is slender and articulates with the epibranchial.

Chambered fin spines. Internal transverse partitions of the fin spines can be seen in radiographs of *Hemiarius, Cephalocassis, Plicofollis* n. gen. *dussumieri, P.* n. gen. *nella, Nemapteryx nenga* and *N. macronotacanthus*. In *Netuma thalassinus* and *Hemiarius dioctes* the spines are half-chambered. Taylor (1986) partly characterised *Ariodes* Müller and Troschel on its chambered spines (his definition however, was based on *Arius dussumieri* (= *Plicofollis* n. gen. *dussumieri)* and not on the type of the genus). This character appears to be very homoplastic.

Barbel form and length. Barbels of inconsistent length and/or various apomorphic morphologies appear to have been independently derived in several catfish lineages. So it is with ariids: in them the barbels may be flattened and strap-like (*Hexanematichthys sagor*), rounded in cross-section (*Nedystoma novaeguineae*), fleshy and flattened (*Arius venosus, A. leptonotacanthus*), wisp-like (cf. *Arius acutirostris*), ribbon like (*Bagre*), stiff and rod-like (*Osteogeneiosus*; *Sciades* species (partly)), or have a low basal membrane (*Cochlefelis spatula, Potamarius*). Barbels may be very long (e.g., cf. *Arius macrorhynchus*) or short (e.g., *Nemapteryx augustus*) and may even vary in length with habitat (*Ariopsis leptaspis*).

Barbel structure may contain phylogenetic information; and Bornbusch (1995: Siluridae) and Chen and Lundberg (1995: Amblycipitidae) briefly discussed barbel structures. I conducted preliminary investigations into the composition of the barbels in representatives of less than twenty Indo-Australian ariid taxa using various staining techniques (mainly Mallory's triple stain and haematoxylin). These investigations revealed that in all taxa except *Hemiarius insidiator* the barbel consists of a central rod of elastin tissue and two lateral rods of collagen fibre. In *H. insidiator* however, there are no collagen rods. Ghiot and Bouchez (1980) found that the barbel of *Pimelodus clarias* (= *Pimelodus blochii*) consists largely of elastin and a single rod of collagen fibres. Study of barbel structure, which is largely lacking (Arratia 1987), may reveal important information on siluroid relationships.

Snout crescent. Roberts (1978) partly diagnosed *Arius cleptolepis* Roberts (= *Ariopsis berneyi* (Whitley)) on its possession of a crescentic snout groove. Such a groove occurs in many ariids and is usually more apparent in juveniles. However, some taxa retain the snout crescent as adults (e.g., *Hexanematichthys mastersi, Arius dispar, Netuma proximus*) and the nominal genus *Selenaspis* is based on the presence of a transverse, flap-covered groove between each pair of nostrils (possibly not homologous with the snout crescent). I am uncertain whether these characters can usefully be employed in a phylogenetic analysis.

Unculi? Roberts (1982) investigated the distribution in ostariophysan fishes of unicellular horny projections, which he termed 'unculi'. These are related morphologically to the multicellular horny tubercles (including nuptial or breeding tubercles) of several groups of fish, among them the Ostariophysi (refer Wiley and Collette 1970). Roberts recorded unculi in six siluroid families (most of them phylogenetically advanced) and they are present in all ostariophysans except gymnotoids. Fink and Fink (1996) also discussed these structures.

Individuals of about half the ariid taxa I examined have tiny elongate soft processes scattered over the snout and sides of the head in adults at all levels of maturity and both sex. Although closer examination using Electron Scanning Microscope techniques was only partly successful, it confirmed that these regularly-shaped structures are not strands of mucus nor artifacts of the fish's preserved condition. Taxa possessing these structures include *Bagre, Galeichthys, Ariopsis leptaspis, Cochlefelis spatula, Cinetodus crassilabris, Hexanematichthys mastersi, Aspistor platypogon, Plicofollis* n. gen. *dussumieri, Cathorops hypophthalmus* and *Hemiarius stormii*. The function of these 'unculi' in the ariids is unknown and should be investigated: they are not associated with breeding. Although presence or absence of these tiny processes may be phylogenetically informative, it would have been premature to evaluate the character in my study, and I lacked fresh material of many taxa having them. The 'cilia' of ictalurids (Lundberg 1982) may/may not be homologous.

Lateral line form. The lateral line in the Ariidae is variable in appearance. In most taxa the line is simple with regularly spaced short branches along its length, but in others (e.g., *Cathorops fuerthii* and *C. hypophthalmus, Cephalocassis melanochir, Cryptarius* n. gen. *truncatus, Bagre bagre* and *Cochlefelis burmanicus*) it is very ramose, especially anteriorly, the venules extending over the shoulder and sides of the head; and in some taxa (e.g., *Plicofollis* n. gen. *crossocheilos*, some *Arius maculatus*) numerous ramifications extend along the whole lateral line. Finally, in some ariids the anterior lateral line sensory tubules are encased in bony plates (e.g., *Cinetodus froggatti, Hexanematichthys sagor*), a condition thought to be plesiomorphic (Arratia 1987; Grande 1987).

Diversity in lateral line form is widespread in catfishes (Howes 1983; Buckup 1988; Ferraris Jr 1988) and is probably correlated with habitat. I did not investigate this in the Ariidae.

Head height and body shape. Although it may not seem so, the general form of the ariid body is quite variable. Some taxa have a depressed head and slender body (e.g., *Sciades* spp, *Hexanematichthys mastersi, H. sagor*) or cylindrical body (e.g., *Brustiarius nox, Cephalocassis*); in others the head (nape) is elevated (e.g., *Batrachocephalus, Cathorops multiradiatus*), or 'dog'-like (e.g., *Potamarius,* cf. *Arius subrostratus*), or spatulate (e.g., *Cochlefelis burmanicus*) or acute (e.g., cf. *Arius acutirostris,* cf. *Arius macrorhynchus*); the caudal peduncle is deeper in *Plicofollis* n. gen. *argyropleuron* and compressed in *Hexanematichthys mastersi*; and the marine *Netuma thalassinus* has a fusiform body.

Fin filaments. A character supporting the genus *Nemapteryx* Ogilby (type species *Arius armiger* de Vis) is the presence of filaments on the fin spines. This phenomenon is not rare in juveniles of many taxa, yet persists in, for example, *Arius maculatus, Nemapteryx armiger, N. nenga* and *Bagre*; also cf. *Arius subrostratus* (Chandy 1953). Retention of fin filaments contains no phylogenetic information in ariids.

Caudal fin shape. Tail shape is variable in siluroids (Lundberg and Baskin 1969). An emarginate shape is derived in ictalurids (Lundberg 1982); and a rounded tail is plesiomorphic in trichomycterids (Arratia *et al.* 1978). The ariid caudal fin is forked or deeply emarginate and the lobes range from being broad and short (e.g., *Amissidens* n. gen. *hainesi*) to narrow and attenuated (e.g., *Netuma thalassinus, Bagre bagre, Brustiarius nox*). In an attempt to quantify caudal fin size, I calculated the ratio between medial and longest outer fin ray in a range of ariids, and found that the medial ray ranges from 2.2–4.3 shorter than the outer ray. However, the results were equivocal. Although not revealed by the ratios, it is plausible that the 'more benthic' taxa have a shallower, broader caudal fin whilst the 'more actively swimming' taxa have a deeply forked and tapered fin.

2. *Meristic and morphometric characters.*

Total number of vertebrae. Stewart (1986a) concluded that the primitive vertebral count for catfishes is between 39 and 45. Nevertheless, whereas this may be a primitive range for siluroids, the range within individual catfish groups may be higher or lower: e.g., 60+ in the clariids (Howes 1983); 30 to 63 in pimelodids (Stewart 1986a); preural vertebral number less than 26 to 37 in the Loricarioidea (Schaefer 1987); 36 to 55 in the Ictaluridae (Grande 1987); and 43 to 67 in the Ariidae. Either a reduced and/or a higher number is considered derived by different authors (e.g., Howes 1983; Stewart 1986;1986a; Schaefer 1987; Ferraris Jr and Fernandez 1987; Kobayakawa 1989).

Lundberg's (1982) observation that species with similar total number of vertebrae can be very different in sectional counts is borne out in the ariids. For example, *Cinetodus carinatus* vertebral count is 17–18 precaudal + 3 haemal + 29–30 caudal, *Bagre* count is 13–15+2–6+29–35, *Cathorops* count is 13–16+3–5+26–32 and in *Sciades* the vertebral count is 18–19+2–6+27–36. I compared preferred habitat and total or sectional vertebral count in ariids, but found no firm correlation. Vertebral counts may be useful at the species level (e.g., between *Netuma thalassinus* and *N. bilineatus* (Kailola 1986)) and I have used it (below) to support the status of some genera and species groups.

Anal fin ray count. Primitive catfishes have 14–16 (†*Hypsidoris*: Grande 1987; Grande and de Pinna 1998) or 11–15 (*Diplomystes*) anal fin rays. Lundberg (1982) suggested that a lower count is relatively more primitive in the ictalurids. Ranges presented in Grande (1987) and Arratia (1987) support this polarity. The most common anal ray count of the ariids lies between 16 and 22, but a few taxa (e.g., *Nedystoma novaeguineae*) have very high counts. Higher anal ray counts have been recorded for autapomorphic auchenipterids and pimelodids (Buckup 1988; Ferraris Jr and Fernandez 1987) and are characteristic of some siluroid families (Grande 1987: Table 2).

Gill raker number. Differences in the gill raker number in fishes generally reflects diet (Lagler *et al.* 1962). Planktivorous fishes have more and slender rakers, whilst predaceous and omnivorous fishes have fewer and stout rakers. Generalised carnivory is widespread among primitive ostariophysans (Lundberg and Mago-Leccia 1986). Roberts (1972) pointed out that most of the survivors of global archaic fish groups are efficient predators. While Fink and Fink (1981) considered that planktivory has evolved independently several times, and Lundberg (1982) stated that extreme gill raker counts are probably derived, W.N. Eschmeyer (in lit., 2003) reasoned well that high gill raker numbers represent the plesiomorphic condition.

Most ariids have a moderate or low gill raker count (9–22) on the leading edge of the first arch, a phenomenon correlating with the dominance of carnivory and omnivory in their diets. However, some taxa (e.g., *Cathorops hypophthalmus, Amissidens* n. gen. *hainesi, Nedystoma dayi, N. novaeguineae*) have more numerous (28–67) rakers. All but the enigmatic *N. novaeguineae* consume fine particles, such as suspended plant material and zooplankton, small insect larvae and fine detritus.

Pectoral fin ray count. Stewart (1986) believed that a higher number (11 or more) of pectoral fin rays is the apomorphic state while Lundberg (1972) and Schaefer (1987) considered that a lower count is derived. Lower counts of segmented rays (6–10) are found in ictalurids (Taylor 1969; Lundberg 1982), some bagrids (Bailey and Stewart 1984), most pimelodids (Stewart 1986a), diplomystids (Arratia 1987), †*Hypsidoris* (Grande 1987) and most loricariids (Schaefer 1987). Tilak (1963) suggested there is a trend in catfishes towards reduction in the number of fin radials and associated rays.

The number of segmented pectoral rays ranges from 8–13 in the Ariidae. Lower counts (8–9) occur in some groups (e.g., *Brustiarius nox*) and higher (12–13) in others (e.g., *Plicofollis* n. gen. *argryopleuron*). Rarely, the count differs between fin pairs of the one individual.

3. *Adaptive characters.*

Form of the jaw teeth. In the vast majority of siluroids, the jaw teeth are simple, conical or tapering structures (Schaefer 1987; pers. obs.). Alexander (1965) observed that the broad band of cylindrical (or cardiform) jaw teeth 'in most unspecialised catfish' are suited for holding food; and Gosline (1973) believed that 'grasping' dentition is ancestral. The teeth in †*Hypsidoris* are simple, sharp-tipped conical structures; those in diplomystids are close-set, elongate and conical with spatulate or pointed tips. All of the outgroup specimens examined have slender, conical or sharp-tipped teeth except for *Pangasius* and the callichthyids which have fine, villiform teeth.

The range of premaxillary and dentary tooth type exhibited in the Ariidae is wide indeed, for example: spatulate or truncate with short cusps (*Ketengus*), truncate and 'peg'-like (*Batrachocephalus*), slightly spatulate (*Cochlefelis*), strong and caniniform (*Hemiarius stormii*), conical with blunt or sharp tips, low and villiform, small and shallowly curved (*Brustiarius*) and molariform (*Cathorops*). I surmise that the more derived ariids possess a dentition *other than* the plesiomorphic condition of conical and slender jaw teeth. This view is supported by my study of ariid diet and feeding morphologies – diets ranging from general to specialised (e.g., molluscivory, frugivory, lepidophagy).

Number of jaw teeth/width of tooth bands. The presumably plesiomorphic siluroid dentition is of moderately broad bands of grasping, usually depressible teeth that frequently point inwards (Gosline 1973, 1975). These teeth work the prey back into the mouth (Alexander 1970) and, for large-mouthed catfishes employing a 'sink' ingestion method, appear to be functionally appropriate. Gosline (1973), who described the 'sink' mechanism (see also Roberts 1972; Howes 1983), determined that feeding in catfishes is done primarily by suction. Examples of siluroids (ariids included) having this dentition and feeding method are numerous.

As well as different tooth form, ariids differ in the relative abundance of teeth on the premaxilla and dentary, and in some taxa adults have more series of teeth than do juveniles. Most wide-mouthed ariids have seven or more (to 16) series of teeth, and ariids with small or moderately narrow mouths have less than eight. Some predaceous, wide-mouthed ariids however, have few (one to six) series of teeth (e.g., *Hemiarius insidiator*, *H. stormii*), a condition which appears to contradict Gosline's (1973) and other authors' feeding theories. However, in four of these taxa, the teeth are non-depressible and wedge-shaped: these fish must seize their prey, the few well-spaced series of powerful teeth being just as or more effective than are numerous series of grasping, slender teeth.

Mouth size, position and lip form. Most ictalurids, ariids, diplomystids, †hypsidorids, many pimelodids, silurids, schilbeids and bagrids have wide mouths, compared to the smaller mouths of, for example, *Pseudodoras* (Alexander 1965), auchenipterids (Mees 1974) and callichthyids. Approximately half of the ariids I studied have a mouth size 37% or more of head length: most of them are predaceous, some also omnivorous as juveniles. However, some ariids have a smaller, almost quadrangular mouth (e.g., *Amissidens* n. gen. *hainesi*) and others have a smaller, inferior mouth (e.g., *Cephalocassis melanochir*, cf. *Arius macrorhynchus*, *Arius microcephalus*): these species sieve detritus and/or algae and detritus in the mid-water column. On the other extreme, *Batrachocephalus* and *Ketengus* have very wide mouths. The jaw symphyses are elevated in some wide-mouthed ariids (e.g., *Nemapteryx armiger*); and in some taxa (e.g., *Bagre*, *Osteogeneiosus*) the mouth is strongly curved.

I consider the narrow-mouthed condition derived within the Ariidae and probably within the Siluriformes – where it has arisen independently in several lineages. The ariids display great variety in lip thickness (soft and fleshy or firm or reduced), snout shape (truncate or rounded or pointed) and mouth position (ventral or terminal or almost superior). All of these characters are associated with habitat and feeding ecology.

Mobility of the jaw teeth. Fink (1981) recognised four types of tooth attachment in actinopterygian fishes. He suggested that the more primitive form is of fixed teeth and there is a predominant trend within the Actinopterygii to evolve teeth with depression mechanisms.

Although investigation of tooth attachment mode was beyond the scope of my study, I consider that in the ariids, where paedomorphic expression of tooth attachment predominates, fixed jaw teeth are the derived character state. This state is exhibited by, for example, *Hemiarius stormii*, *H. dioctes* and *Nemapteryx augustus* and is correlated with large mouth, predatory habit and macroscopic diet.

Eye position and size. The usual siluroid eye position is superolateral; however Howes (1983) noted several unrelated siluroids having a ventrolaterally situated eye: *Hypophthalmus*, *Ageneiosus*, some species of *Auchenipterus* and *Pangasius*; also *Ompok* (pers. obs.). A ventrolateral eye is derived also in the Ariidae: the best examples are *Nedystoma novaeguineae* and *Cathorops hypophthalmus*; and probably a superior eye (e.g., as in *Ketengus*) is also derived.

Eye size varies both inter- and intraspecifically and there is an overall trend in the Australo-Papuan ariids for negative allometry in eye size. However, in, for example, *Hemiarius insidiator*, *Nemapteryx augustus* and *Ariopsis coatesi* the eye is consistently small relative to head length at all growth stadia (mean less than or equal to 11% head length), suggesting that these taxa inhabit waters with fast currents (Roberts and Stewart 1976).

Papillae on rear of gill arches. Orobranchial papillae appear to have evolved independently in several catfish lineages. They occur in the Diplomystidae, Nematogeniidae (Howes 1983a; Arratia 1987), some Pimelodidae (Stewart and Pavlik 1985; Stewart 1986a) and several Ariidae including *Guiritinga barbus*, some *Cathorops*, *Ariopsis velutinus*, *Plicofollis* n. gen. *nella* and *Cinetodus crassilabris*. Other ariids have papillae on the palate only – for example *Arius manillensis*, *Plicofollis* n. gen. *dussumieri* and *Aspistor luniscutis*. In *Cephalocassis melanochir* the raker-less backs of the first two arches are densely covered with papillae formed into about two rows.

Roberts' (1972) observation, that planktivorous and carnivorous fishes have smooth palates and gill arches compared to detrital feeders, applies to the ariids. However, I suspect that some omnivorous and predaceous taxa possess papillate surfaces at juvenile stadia only, the papillae not being required as the fish's diet changes with growth.

A distinct arrangement of the papillae and fleshy ridges form a synapomorphy for three pimelodid genera (Stewart and Pavlik 1985). H. Higuchi (pers. comm.) reported that gill arch papillae in some doradid taxa are provided with taste buds.

Gut shape. I examined the Australo-Papuan taxa with a view to recognising differential gut forms following the lead of Merriman's (1940) study of *Bagre marinus* and *Ariopsis felis*. Difference in intestinal convolutions has been used successfully to distinguish other fish groups (e.g., the Scombridae: Collette and Russo 1985).

However, presence/absence of food in the gut and quality of specimen fixation affected the appearance of this character in the specimens I examined. Nevertheless, I found both more and less-convoluted gut forms in the ariids I examined; for example, very convoluted in *Netuma thalassinus* and *Bagre marinus*, and almost straight in *Hemiarius dioctes* and *Cathorops fuerthii*.

Identification of valid ariid genera, natural subgroups and phylogenetic relationships of ariid taxa. One cladogram is presented (Fig. 15 A, B), a strict consensus of 972 trees from the PAUP* 4 beta 10

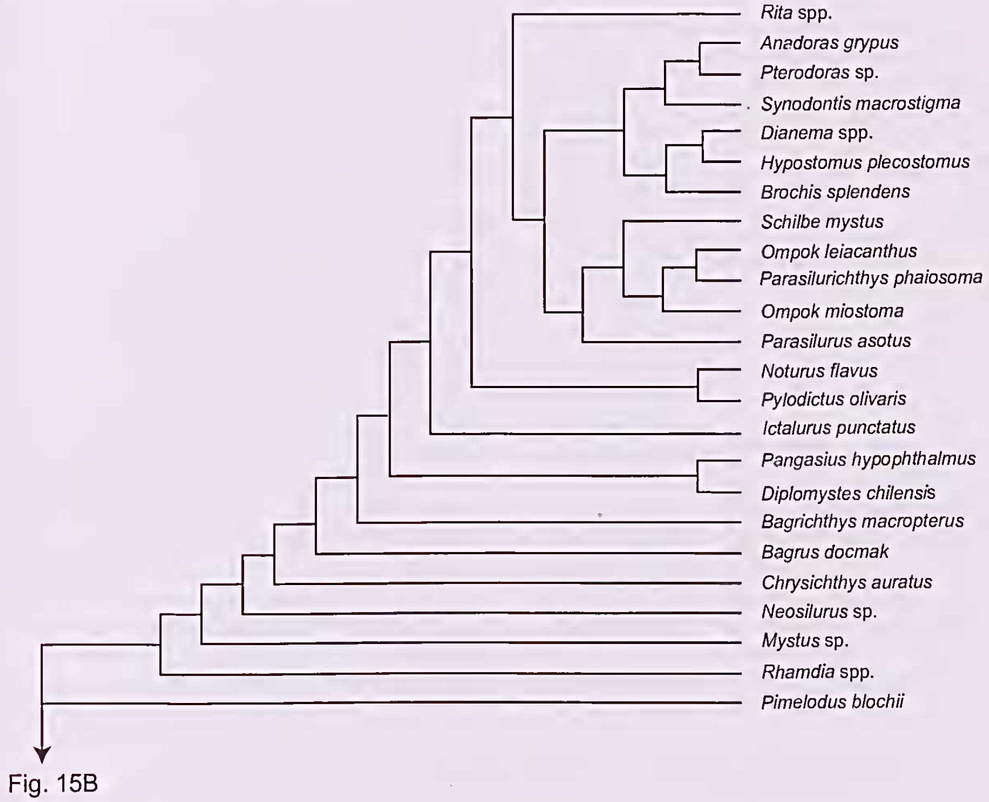

Fig. 15. Strict consensus tree of 972 trees, of 78 taxa, consistency index of 0.749, characters unordered and of equal weight, heuristic search (TBR): A, outgroup taxa.

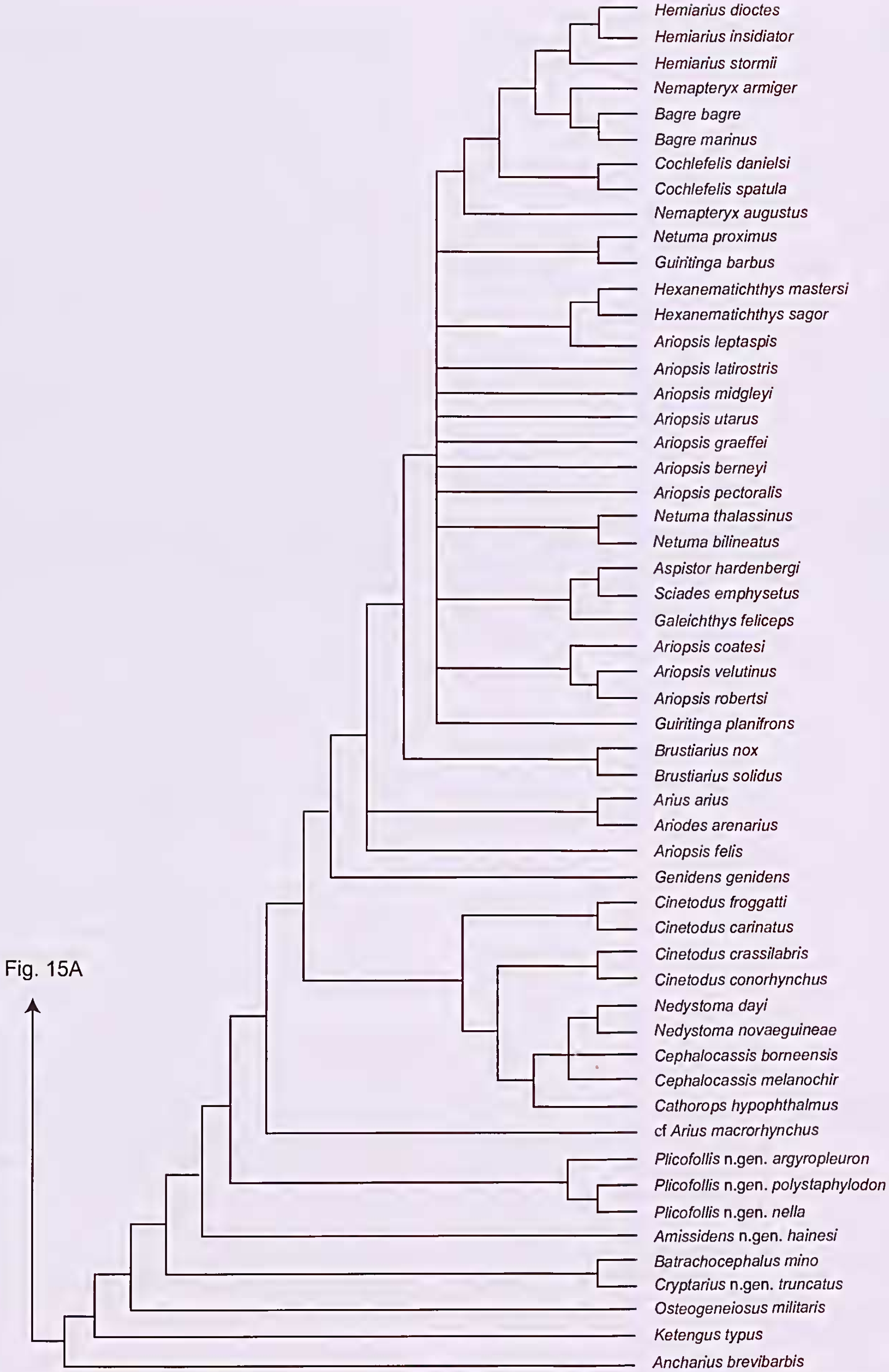

Fig. 15. Strict consensus tree of 972 trees, of 78 taxa, consistency index of 0.749, characters unordered and of equal weight, heuristic search (TBR): **B**, ingroup taxa.

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analyses. PAUP* 4 beta 10 found that two characters were uninformative. These are character 40 (secondary hypurapophysis) and character 52 (dentition on palate tooth plates).

The results of the phylogenetic analysis of 57 characters, spread over 54 ingroup (ariid) and 24 outgroup OTUs have led to a revised, and consolidated, generic classification of the Ariidae. This revised classification is supported by synapomorphies revealed from phylogenetic reconstruction, by associated meristic and morphological information, and by sets of homoplastic characters. The robustness of my revised classification of the Ariidae is evidenced by my testing the phylogeny revealed by an older version of PAUP (Kailola 1990) with this recent version. The phylogenetic analyses made by PAUP* 4 beta 10 led me to better accommodate only *Cryptarius* n. gen. *truncatus*, *Batrachocephalus mino*, *Guiritinga* and *Ariopsis* species.

Polarity, tree analysis and homoplasy. A recurring problem with the use of outgroup comparison for determining character polarity is the requirement that the interrelationship of the ingroup and outgroup is known, something not available for the Ariidae. Selection of outgroups for any catfish family can best be described as haphazard: almost all catfish families could be nominated as outgroups to the Ariidae as only about half of the known catfish families have been systematically reviewed since Regan (1911). Most of those that have been reviewed constitute the larger, or 'more specialised', or more accessible groups. Thus, because polarity assessment is more robust the closer and more comprehensive the outgroup (Maddison *et al.* 1984), polarities in this study are necessarily more fragile.

Resolution of the polarity matter in this study resulted in my selecting a functional outgroup (*fide* Watrous and Wheeler 1981; Arnold 1981) on several levels, following the examples of authors such as Lundberg (1982), Weitzman and Fink (1985), Arratia (1987), Schaefer (1987) and Vari (1989), *viz*: a generalised outgroup of siluroids, ostariophysans and plesiomorphic teleosts (e.g., Fink and Fink 1981) under the assumption that the state of an homologous character most widespread among them (but not including all or part of the ingroup) is plesiomorphic. Recourse to this 'wider net' of taxa was particularly helpful when (a) only equivocal polarity assessment was reached from comparison with presumably more closely related taxa; (b) assessing the character state in eight possibly closely related and presumably holistic (Howes 1985; Lundberg *et al.* 1988) catfish families (Bagridae, Pimelodidae, Doradidae, Synodontidae, Siluridae, Pangasiidae, Ictaluridae and Schilbeidae); (c) comparing the two recognised sister groups to the Siluroidea (Grande 1987): the Diplomystidae and the extinct †Hypsidoridae; (d) using the 'predominant-states' method (Kluge and Farris 1969; Arnold 1981; Maddison *et al.* 1984).

Although my use of ontogenetic transformation series to assess polarity was restricted because few very small specimens were available, ontogenetic precedence was the sole polarity criterion when morphological homologues were absent in outgroups (e.g., subvertebral cone development, palatal dentition).

The effect of using ariids from different world regions (where homoplasy remained high) to determine the extent of convergence within the family Ariidae merely confirmed that the convergences revealed are real. In the earlier analyses (Kailola 1990) the trees in which homoplasy was higher were those constructed from mainly ariid taxa, while those trees constructed from fewer ariid taxa plus the outgroup exhibited less homoplasy. The mixes of ariid taxa in the earlier analyses revealed that convergences and parallelisms of character states are common to all members of the family, not just to Australo-Papuan members.

Sets of taxa consistently grouped at approximately comparable positions on earlier (Kailola 1990) and recent (this work) consensus trees. For example, of Australo-Papuan taxa, *Nedystoma dayi* + *N. novaeguineae*; *Cinetodus crassilabris* + *C. froggatti* + *C. carinatus* always established proximally and *Hemiarius dioctes* + *H. insidiator* established distally. When extralimital taxa were incorporated in analyses with Australo-Papuan taxa the results revealed the following ('higher-level') clusters: *Bagre* + *Ailurichthys*; *Arius* + *Ariopsis*, usually + *Ariodes*; *Batrachocephalus* + *Cryptarius* n. gen. *truncatus*; *Hemipimelodus* + *Cephalocassis*; *Hemiarius* + *H. dioctes* + *H. insidiator*; *Hexanematichthys* + *H. mastersi*; *Sciades* + *Aspistor hardenbergi*; *Cathorops* + *Hemipimelodus* + *Cephalocassis* + *Nedystoma novaeguineae* + *N. dayi*. However, the most parsimonious position of several individual taxa was inconsistent in all analyses and could not be resolved. These taxa include *Nemapteryx armiger, Netuma proximus, Guiritinga barbus, Ariopsis utarus, Genidens genidens*, cf. *Arius macrorhynchus* and *Amissidens* n. gen. *hainesi*.

The weaving play of homoplasy in the family Ariidae is most remarkable. No one genus stands unequivocally on its own derived character states (autapomorphies): homoplastic characters make definite contributions to the composition of each. The spread of homoplasy through the family also – to me – underscores the commonality of the ariid ancestral stock. Ariid taxa draw on a suite of characters which often already exist: if they can be useful in a habitat, they are used; if not useful, they are not used (but still exist, somewhere, and can be drawn upon by another taxon, in another place); occasionally they appear to occur as non-contributing characters.

Clades are largely supported by homoplastic characters (below). This 'homoplastic' situation in

Ariidae appears unusual among catfishes: for example, in a study of phylogenetic relationships among the Auchenipteridae, Curran (1989) was able to tighten his data set such that only one homoplastic character remained!

Characters in which the states were frequently switched in the most parsimonious tree reconstructions include fin spine thickness, size of adipose fin, palatal flap development, posterior cleithral process size, mesethmoid shape, nasal shape, gill opening width, abdominal cavity length, first infraorbital (lachrimal) shape, posterior gill raker disposition and lateral line direction. It is remarkable that homologues of a number of these characters have been used 'successfully' in phylogenetic reconstructions of other siluroid families (e.g., the Ictaluridae, Chacidae, Loricariidae, Diplomystidae) where they rarely exhibit *any* homoplasy! The 'reliance' of ariid classification on homoplastic characters, and the hitherto unsuspected close relationship of taxa from widely separated geographic regions are illustrated below.

- *Hexanematichthys sagor* (South-east Asia) and *H. mastersi* (southern New Guinea and Australia) share the derived character of reduction of the temporal fossa (as do, for example, *Guiritinga barbus* (South America), *Brustiarius nox* (northern New Guinea), *Batrachocephalus* (South-east Asia), *Aspistor kessleri* and *A. platypogon* (central America), *Cephalocassis melanochir* (Borneo) and *Cathorops* (central and south America)) and the synapomorphy of dark peritoneum (as do some taxa of *Ariopsis* (Americas)).
- *Hemiarius stormii* (South-east Asia), *H. dioctes* and *H. insidiator* (southern New Guinea and northern Australia) form a clade supported by several derived states including a convex mesethmoid (also in, e.g., *Netuma thalassinus* (Red Sea to Australia), *Bagre* (central and south America), *Nedystoma novaeguineae* (southern New Guinea), *Batrachocephalus* and *Cryptarius* n. gen. *truncatus* (South-east Asia), thickened fin spines (not *Hemiarius insidiator*) (also in *Batrachocephalus* and *Nemapteryx nenga* (India to Asia)), enlarged mandibulary pores (also in, e.g., *Cinetodus* (southern New Guinea and Australia) and *Bagre*), an extensive metapterygoid and well-staggered chin barbels (also in, e.g., *Nemapteryx armiger* (southern New Guinea and Australia), *Sciades* (South America) and *Nedystoma novaeguineae*).
- The synapomorphies of smooth neurocranium (also in *Galeichthys* (southern Africa and South America) and *Cephalocassis*) and reduced gonad unite *Nedystoma dayi* (southern New Guinea) and *N. novaeguineae*. *Nedystoma* also has more gill rakers on the first arch than have all other taxa except for *Brustiarius nox*, *Cathorops hypophthalmus* and *Amissidens* n. gen. *hainesi* (southern New Guinea and Australia).
- The synapomorphy of a dark buccopharyngeal cavity supports the *Brustiarius nox* and *B. solidus* (northern New Guinea) clade. Other taxa having this derived character state are *Amissidens* n. gen. *hainesi* (New Guinea individuals) and *Aspistor platypogon*.
- Possession of tiny mandibulary pores (also in taxa such as *Batrachocephalus*, *Potamarius* (central America), *Aspistor hardenbergi* (southern New Guinea) and *A. luniscutis* (Brazil)) and a convex mesethmoid link *Cochlefelis danielsi* with *C. spatula* (southern New Guinea).
- The taxa *Plicofollis* n. gen. *argyropleuron*, *P.* n. gen. *nella*, *P.* n. gen. *polystaphylodon*, *P.* n. gen. *dussumieri*, *P.* n. gen. *crossocheilos*, *P.* n. gen. *layardi* and *P.* n. gen. *magatensis* (East Africa and India to South-east Asia, Australia) are distinguished by the derived states of vertically narrowed caudal vertebrae (not in all taxa; also in *Bagre*), longitudinally-arranged posterior palatal tooth plates, scalloped margin to swim bladder (also in *Netuma thalassinus*, *N. proximus* (southern New Guinea and Australia), *Cryptarius* n. gen. *truncatus*, *Osteogeneiosus* (South-east Asia), *Hemiarius* and *H. dioctes*) and 'club'-shaped vomer.
- The character state of the independent epioccipital in the skull roof is present in *Plicofollis* n. gen. *argyropleuron*, *P.* n. gen. *nella*, *P.* n. gen. *dussumieri*, *P.* n. gen. *polystaphylodon*, *Netuma proximus*, *Bagre*, *Aspistor luniscutis*, *Hemiarius sona* (India) and *Cryptarius* n. gen. *truncatus*. Earlier analyses (Kailola 1990) placed *Netuma proximus* either with *Aspistor hardenbergi* (epioccipital in the skull roof) or with *Netuma bilineatus* (India to Australia) and *N. thalassinus*. Whereas only two homoplastic characters – bifurcate lateral line and few posterior gill rakers – supported the pairing of *N. thalassinus* and *N. bilineatus*, the common character states of scalloped swim bladder shape, small and posterior adipose fin and absence of posterior gill rakers group these species with *N. proximus*.
- The *Cinetodus froggatti* + *C. carinatus* and *C. crassilabris* + *C. conorhynchus* (all southern New Guinea) pairs are supported by the derived character states of extrascapular fusion with the epioccipital (also shared with *Cathorops*) and a long posterior cleithral process.

An example of how the sharing of many convergences does *not* indicate a common phylogeny however, is best illustrated by *Cathorops*, *Nedystoma*, *Hemipimelodus* (Mekong River drainage to Borneo), *Cephalocassis* and *Cinetodus crassilabris*. These taxa share many convergences (an elevated subvertebral cone, a restricted gill opening (not *Nedystoma novaeguineae*), and small posterior cleithral process (not *Cinetodus crassilabris*)) and often the synapomorphies of high fourth neural spine-epioccipital flanges, pad-less female pelvic fins, an open posterior dorsomedian fontanelle, an apomorphic frontal size and extensive laminar bone. However, *Hemipimelodus*, *Cephalocassis*, *Nedystoma novaeguineae* and *Cathorops* often have an almost skin-covered eye, and a rounded open posterior dorsomedian fontanelle (as also has *Nedystoma*). Only *Cathorops* and *Cinetodus* species possess a united extrascapular and epioccipital. The epioccipital invades the roof of the neurocranium in the geographically widely separated taxa of, for example, *Cathorops*, *Plicofollis* n. gen. *nella*, *P.* n. gen. *polystaphylodon*, *Aspistor luniscutis* and *Cryptarius* n. gen. *truncatus*. Although *Cathorops* is distinguished by several autapomorphies, the highly-developed flanges at the back of the neurocranium and the well-developed and intrusive epioccipital tend to support a closer relationship between *Cathorops* and *Cinetodus crassilabris*; and the relationship of these taxa with the phenetically similar *Potamarius* should also be investigated. *Cathorops*, *Hemipimelodus*, *Cephalocassis* and *Cinetodus crassilabris*, possessing two distinct ovaries and sexually mature females having padded pelvic fins, currently place no closer relationship between them and *Nedystoma* than sister taxa however.

Sometimes I have refrained from nominating a higher taxonomic level to species groups based only on homoplasies. Such is the case of six Australo-Papuan taxa which I place here in *Ariopsis*: perhaps later studies will identify characters to prove or disprove the allocation. The first group of taxa (*Ariopsis velutinus* + *A. robertsi* + *A. coatesi*) have in common a moderately large subvertebral cone, an untoothed vomer, apomorphic frontal size (not *A. velutinus*), the posterior dorsomedian fontanelle always open, no toothed plates on the palate (not *A. coatesi*) and gill rakers present on the trailing edge of the second through fourth gill arches. The second group of taxa (*Ariopsis graeffei* + *A. berneyi* + *A. pectoralis*) share a moderately wide gill opening, either no or unstable patches of vomerine teeth variably present or absent, rakers present on the trailing edge of all gill arches and some individually derived character states (e.g., moderate buccopharyngeal pads in *A. berneyi*).

My study showed that there is almost no difference between the nominal genera *Arius* (and *Pseudarius*) and *Ariodes* and *Neoarius* (India to South-east Asia and Australia), *Ariopsis*, *Genidens* and *Guiritinga* (Americas). Apart from dentition, the only characters that differentiate the taxa are the more homoplastic characters of relative extent of the gill openings, relative size of the subvertebral cones, buccopharyngeal ornamenture, size and shape of the temporal fossa, posterior dorsomedian fontanelle, frontal, post-cleithral process, adipose fin and mesethmoid, position of the metapterygoid, presence of posterior rakers, and final direction of the lateral line. In my original study (Kailola 1990) I excluded form of the jaw (and palatal) teeth from analysis on the basis that they are ecologically adaptive characters, correlated with diet. However, early authors (Bleeker 1863; Günther 1864; Day 1877) used the form of the palatal teeth as a major character in classifications: Bleeker (1863) and Günther (1864) re-defined eighteen nominal ariid genera or ordered the family, on the basis of palatal teeth form, disposition and presence; and Day (1877: 456) considered that whether palatal teeth are villiform or granular 'forms a good method of division'.

Polarity for tooth form can be assigned on the assumption that the more plesiomorphic ariids possess teeth that are conical and slender (Alexander 1965; Gosline 1973; Roberts 1973; Arratia 1987; siluroid outgroup material). The type species of *Arius* (and *Pseudarius*) has granular (or molar-like, or blunt and conical) teeth on the palate, as has the type species of *Ariodes*. *Ariopsis* has fine and sharp teeth on the palate, as has *Neoarius* (type species *Arius curtisii* Castelnau). *Guiritinga* (type species *Pimelodus commersonii* Lacépède, = *Pimelodus barbus* Lacépède) has fine and conical, sharp palate teeth, and *Genidens* has conical palate teeth.

Key to genera of Ariidae

(Note: *incertae sedae* taxa are not included)

1a. Three pairs of barbels around mouth 4
1b. Less than three pairs of barbels around mouth 2
2a. No maxillary barbels .... *Batrachocephalus*
2b. Pair of maxillary barbels 3
3a. Maxillary barbels long and stiff; neurocranium heavily ossified .... *Osteogeneiosus*
3b. Maxillary barbels flexible, long and strap-like; neurocranium weakly ossified .... *Bagre*
4a. Buccopharyngeal pads and flaps well-developed; no teeth on palate; barbels thin and short (29–56% HL), only just reaching past eye; 28–37 rakers on first gill arch; fin spines thin .... *Amissidens* n.gen.
4b. Combination not as above 5
5a. No teeth on palate 6
5b. Teeth on palate (may be difficult to find in brooding males) 10
6a. Mouth wide, extending well past eye; barbels equal to or shorter than eye diameter; single series of incisor-like, sometimes spatulate, teeth in strongly ossified jaws; only one frontal-lateral ethmoid extension (each side) .... *Ketengus*
6b. Mouth small; jaw teeth not as above; two frontal-lateral ethmoid extensions (each side) 7
7a. Buccopharyngeal pads and flaps poorly-developed; subvertebral cone low; barbels short; eyes placed high on head .... *Potamarius*
7b. Buccopharyngeal pads and flaps well-developed; subvertebral cone moderate to high 8
8a. Total gill rakers (first arch) 29–43 ... *Nedystoma*
8b. Total gill rakers (first arch) 11–19 9

9a. No pads on inner pelvic fin ray; supraoccipital process broadly triangular; extrascapular and epioccipital united and exposed in skull roof; eye free of skin .... *Cinetodus*

9b. Pads on inner pelvic fin ray in mature females; supraoccipital process narrow; epioccipital not in skull roof; eye covered by skin .. *Cephalocassis*

10a. Teeth on palate granular (molariform or coarse or conical and usually blunt, 'peg'-like) 11

10b. Teeth on palate fine, or as narrow cones with sharp tips, or spatulate 13

11a. Teeth in lower jaw fine; subvertebral cone low; flanges and ridges from epioccipital, fourth neural spine and vertebra lamina usually poorly developed; epioccipital not in skull roof; 9–15 thoracic vertebrae 12

11b. Molariform teeth in inner row on mandible in some species; subvertebral cone high; flanges and ridges from epioccipital, fourth neural spine and laminae of anterior fused vertebrae high and extensive; epioccipital invades skull roof and is amalgamated with extrascapular; 7–10 thoracic vertebrae .... *Cathorops*

12a. Single patches of granular teeth on each side of palate; rakers present along back of all gill arches; vomer 'T'-shaped; hind margin of metapterygoid aligned with hind margin of quadrate; swim bladder sides smooth .... *Arius*

12b. Two patches of granular teeth on each side of palate, longitudinally arranged; rakers absent from back of first gill arch and often second; vomer comprises an enlarged, rounded 'head' and short arms; metapterygoid enlarged and extending well beyond hind margin of quadrate; swim bladder sides usually scalloped or creased .... *Plicofollis* n.gen.

13a. Jaw teeth sharp, fixed, non-depressible; jaws strong, lower jaw at symphysis directed upwards; chin barbel bases widely spaced; eye small (and may be covered by skin) 14

13b. Jaw teeth villiform or fine and conical, depressible; remaining combination not as above 16

14a. A 29–33; GR (first arch) 45–51 .... *Nedystoma*

14b. A 15–25; GR (first arch) 12–22 15

15a. Swim bladder smooth-edged; mesethmoid truncate; posterior dorsomedian fontanelle usually deep and 'tear-drop' shaped; barbels long (not in *N. augustus*); adipose fin short-based; dorsal fin spine bears a filament at all stadia . *Nemapteryx*

15b. Swim bladder edge scalloped or creased; mesethmoid convex; posterior dorsomedian fontanelle shallow; barbels short (mandibulary long in *H. insidiator*); adipose fin long-based (not in *H. insidiator*) .... *Hemiarius*

16a. Adipose fin short-based and situated above second half of anal fin; caudal fin lobes slender and attenuated; body dark, or fusiform 17

16b. Combination not as above 18

17a. 8–10 pectoral fin rays; 19–67 rakers on first gill arch; jaws thin and upturned at symphysis; 9–13 thoracic vertebrae; swim bladder smooth-sided .... *Brustiarius*

17b. 10–12 pectoral fin rays; 10–16 rakers on first gill arch; jaws terminal or subinferior; 12–15 thoracic vertebrae; swim bladder sides scalloped .... *Netuma*

18a. Head broad; head shield usually extensive, granular or rugose; frontal bone broad anteriorly, space between frontal and lateral ethmoid may be reduced or absent; posterior dorsomedian fontanelle absent or very small; supraoccipital usually broad and short; nuchal plate usually expanding with age 19

18b. Combination not as above 21

19a. Peritoneum dark or spotted dark; adipose fin long-based, spanning all of anal fin; 12–18 rakers on first gill arch; 13–18 thoracic vertebrae; no parasphenoid/orbitosphenoid teeth .... *Hexanematichthys*

19b. Combination not as above 20

20a. Subvertebral cone high; mesethmoid with two diverging, curved cornuae; nasal bone simple and rod-like; 11–15 rakers on first gill arch; 5–12 thoracic vertebrae; swim bladder as one chamber .... *Aspistor*

20b. Subvertebral cone moderately low; mesethmoid truncate and stout; nasal bone curved; 16–24 rakers on first gill arch; 11–20 thoracic vertebrae; swim bladder in two chambers .... *Sciades*

21a. Gill openings wide or moderately so; chin barbel bases not close together nor transversely aligned 22

21b. Gill openings restricted, not open across isthmus; chin barbel bases close together and aligned 24

22a. Epioccipital short, not contacting dorsal surface of bone overlying anterior complex vertebrae; exposed supraneural present between supraoccipital and nuchal plate; posterior cleithral process broad and fan-shaped; neurocranium almost smooth; no pads on pelvic fins of mature females .... *Galeichthys*

22b. Combination not as above 23

23a. Head depressed; teeth in upper jaw in broad, curved band, band exposed beyond lower jaw; adipose fin long-based, equal to length of anal fin base; tiny mandibulary pores ...... *Cochlefelis*

23b. Combination not as above .... *Ariopsis*

24a. Epioccipital in skull roof united with extrascapular to form one bone; no pads on pelvic fins of mature females; neurocranium thick and supraoccipital broadly triangular .... *Cinetodus*

24b. Epioccipital in skull roof (or almost) as an extra bone to extrascapular; neurocranium not especially thick and supraoccipital not broadly triangular 25

25a. Buccopharyngeal pads and flaps well-developed; laminar bone over anterior fused vertebrae extensive; posterior dorsomedian fontanelle heart-shaped or rounded; subvertebral cone strong and high .... *Cephalocassis*

25b. Buccopharyngeal pads and flaps poorly developed; deeply excavated laminar bone over anterior fused vertebrae; posterior dorsomedian fontanelle elongate; subvertebral cone moderately high .... *Cryptarius* n.gen.

Revised classification of Ariidae

Amissidens new genus

Type species: *Arius hainesi* Kailola 2000: 139, by monotypy.

Diagnosis. *Amissidens* is characterised by the combination of toothless palate (although autogenous tooth plates are present), deeply excavated and elongate dorsomedian fontanelle, two large epithelial flaps on the palate posteriorly and double folds of epithelial tissue on the upper limb of the first two gill arches, and rakers present along the back of all gill arches. Pads on the pelvic fins of mature females are scalloped and tapered and the gonads in females are united along their proximal third. The metapterygoid is enlarged and ends well past the hind border of the quadrate, and the fin spines are thin, long and slender.

The frontal-lateral ethmoid space is large and the lateral ethmoid is prominent. The palatines are long, the jaws are thin, and the premaxillary is short with truncate lateral margin. The laminar bone over the anterior vertebrae is extensive, and the Mullerian ramus is long. The triangular supraoccipital process has a prominent median keel. The short posterior cleithral process is heavily ossified anteroventrally.

The jaw teeth are slender, in a short, oblong band; the lips are fleshy and thin and the mouth is small and almost quadrangular; all of the premaxillary tooth band is visible when the mouth is closed. A shallow groove is usually present on the snout between the posterior nostrils. The barbels are thin and wisp-like distally, the longest reaching only past the eye, 29–56% HL; the bases of the chin barbels are close together and aligned transversely. The eye is large, 14–24% HL. The gill openings are somewhat restricted and there are many (28–37) gill rakers. The adipose fin is short-based and situated posteriorly. The lateral line turns dorsad at the tail base. The branchial chamber and sometimes the hind part of the mouth often are coloured dark brown or purplish charcoal. Seven to ten longitudinal ridges or furrows develop in the skin of the nape and upper sides with growth.

Br 6. A. 20–23. P. I,10–11. Total gill rakers (first arch) 28–37. Vertebrae 6–7+10–11+3–5+27–29, total 49–50.

Etymology. From *ammissus* (Latin) meaning lost, and *dens* (Latin) meaning teeth (Brown 1956) in reference to the type species having autogenous tooth plates which lack the teeth they usually bear in other taxa.

Comparisons. *Amissidens* shares with *Nedystoma* and *Brustiarius* character states such as a high number of gill rakers (28–37; 29–51 in *Nedystoma*; 19–67 in *Brustiarius*), thin jaws, and short-based adipose fin. *Amissidens*, *Nedystoma dayi* and *Brustarius nox* have well-developed buccopharyngeal flaps and pads, epithelial folds around and before the anterior gill arches, and short-based adipose fin. With *Brustiarius*, *Amissidens* shares the presence of pelvic fin pads in mature females and moderately high subvertebral cone, reduced gonad and dark buccopharyngeal cavity (also in *Aspistor platypogon*). With *Nedystoma* it shares posteriorly broad frontals with narrow anterior arms. *Nedystoma dayi* and *Cryptarius* n.gen. also have a restricted gill opening and *N. dayi* has a toothless palate. Apomorphies of *Amissidens hainesi* are shared with representatives of other genera: a long Mullerian ramus (with *Hemiarius dioctes*, *Cinetodus*, *Nedystoma dayi*); a conspicuous and irregularly-shaped dorsomedian fontanelle (with *Nemapteryx armiger*). The proximal third of the gonads in females are united also in *Cryptarius* n. gen. *truncatus*.

Distribution. Sahul Shelf (southern New Guinea, northern Australia). Near-shore coastal waters to tidal reaches of rivers.

Taxa. One species: *Amissidens hainesi* (Kailola, 2000).

Ariopsis Gill, 1861

Ariopsis Gill, 1861: 56 (type species, *Arius milberti* Valenciennes, 1840a, by monotypy).

Neoarius Castelnau, 1878: 237 (type species, *Arius curtisii* Castelnau, 1878, by monotypy).

Diagnosis. *Ariopsis* is characterised by having villiform or sharp, fine conical teeth on the palate in one or two patches on each side, or rarely, no teeth; in combination with the lateral line turning upwards at the tail base, the subvertebral cone being low or moderate-sized, the buccopharyngeal pads being low or moderate-sized and the adipose fin of moderate size and above the middle of the anal fin.

The ridges and lamellae of the epioccipital are low to well elevated (*Ariopsis felis*). The mesethmoid is notched with short or broad cornuae, and the nasal bone is simple, either straight or curved. The vomer is 'T'-shaped. The pores on the mandible are small (*A. felis*) to moderately large. The epioccipital does not enter the skull roof. The temporal fossa is either prominent at all growth stadia (e.g., *A. graeffei*) or tending to reduce with growth (*A. felis*). The metapterygoid hind margin is above the middle of the quadrate except in *A. felis* where it is in line with the hind margin of the quadrate. When present, the posterior dorsomedian fontanelle is elongate. The frontal is either narrow or broad posteriorly (*A. robertsi, A. coatesi*), and the laminar bone of the anterior vertebrae covers the bases of the fourth to sixth transverse processes.

Sometimes there are no teeth on the palate (see below) and the gill openings range from wide to moderately wide (*Ariopsis berneyi, A. felis*). Rakers may be present along the back of all gill arches (e.g., *A. graeffei*), absent from the first (e.g., *A. latirostris, A. utarus*) or absent from first and second (e.g., *A. felis, A. leptaspis*). The chin barbel bases are neither close together nor widely separated. Mature females develop pads on the inner pelvic fin rays; the swim bladder is ovate or heart-shaped, and the female gonad is bilobate. The fin spines are robust, thick and serrated and the skull surface is granular to rugose.

Ariopsis felis: Br 6. A. 15–17. P. I,10–11. Total gill rakers (first arch) 13–16. Vertebrae 7+11–12+6–8+27–29, total 53–54.

All species: Br 6. A. 14–24. P. I,9–12. Total gill rakers (first arch) 10–33. Vertebrae 7+10–15+5–8+25–30, total 49–56.

Comparisons. Most species have patches of teeth on the vomer and on the palatines, and the shape and relationship of the tooth patches varies, the tooth patches often enlarging with age. Four Sahul Shelf taxa (*Ariopsis pectoralis, A. velutinus, A. robertsi, A. coatesi*) lack vomerine teeth, and two of these (*Ariopsis velutinus, A. robertsi*) also lack palatine teeth. Such species previously were included in the nominal genus *Hemipimelodus* Bleeker because of that trait (Weber and de Beaufort 1913; Désoutter 1977; Roberts 1978). In some American taxa (e.g., *Ariopsis seemani, A. guatemalensis*) the axil and upper surfaces of the pectoral and pelvic fins are dusky or bluish (as in *Cinetodus*), the barbels are darkly pigmented, and (in *Ariopsis seemani*) the peritoneum is stippled black, sometimes densely (as in *Hexanematichthys*, and *Arius oetik*).

The PAUP analyses consistently identified two groups of *Ariopsis* within the Sahul Shelf complement: *Ariopsis berneyi, A. graeffei* and *A. pectoralis* in one group, and *A. coatesi, A. robertsi* and *A. velutinus* in the other (Fig. 15).

No significant character states in my matrix distinguished *Guiritinga barbus* (Lacépède, 1803) and *G. planifrons* (Higuchi, Reis and Araujo, 1982) from the taxa I am placing in *Ariopsis*. Even so, I identified several character states (unscored) in *G. barbus* and *G. planifrons* that are not present in these *Ariopsis* taxa (see Incertae sedae below for more discussion).

Distribution. Central America, south-eastern North America, northern South America, New Guinea and Australia. Inshore coastal, estuarine and fresh waters.

Taxa. About nineteen valid taxa. Eleven taxa from the Sahul Shelf: *Ariopsis berneyi* (Whitley, 1941) (synonym: *Arius cleptolepis* Roberts, 1978); *A. coatesi* Kailola, 1990a; *A. graeffei* Kner and Steindachner, 1866 (synonyms: *Arius australis* Günther, 1867; *Arius curtisii* Castelnau, 1878); *A. leptaspis* (Bleeker, 1862); *A. latirostris* (Macleay, 1884) (synonyms: *Arius acrocephalus* Weber, 1913; *Arius digulensis* Hardenberg, 1936); *A. midgleyi* (Kailola and Pierce, 1988); *A. paucus* (Kailola, 2000); *A. pectoralis* (Kailola, 2000); *A. robertsi* (Kailola, 1990a) (synonym: *Arius taylori* Roberts, 1978); *A. utarus* (Kailola, 1990a); *A. velutinus* (Weber, 1908) (synonym: *Hemipimelodus papillifer* Herre, 1935). American taxa are: *A. assimilis* (Günther, 1864); *A. bonillai* (Miles, 1945); *A. felis* (Linnaeus, 1766); *A. guatemalensis* (Günther, 1864) (synonyms: *Arius caerulescens* Günther, 1864; *Galeichthys azureus* Jordan and Williams in Jordan, 1895); *A. insculptus* (Jordan and Gilbert, 1883); *A. lentiginosus* (Eigenmann and Eigenmann, 1888) (synonym: *Galeichthys xenauchen* Gilbert in Jordan and Evermann, 1898); *A. seemanni* (Günther, 1864) (synonyms: *Tachisurus jordani* Eigenmann and Eigenmann, 1888; *Galeichthys gilberti* Jordan and Williams in Jordan, 1895; *G. eigenmanni* Gilbert and Starks, 1904; *G. simonsi* Starks, 1906); *A. surinamensis* (Bleeker, 1862a).

It is tempting to include three Madagascar species (*Arius madagascariensis* Vaillant, 1894, *Arius festinus* Ng and Sparks, 2003 and *Arius uncinatus* Ng and Sparks, 2003) in *Ariopsis*. I have seen limited material of *A. madagascariensis* only.

Literature synonyms of *Ariopsis felis* are *Arius equestris* Baird and Girard, 1854; *Galeichthys guentheri* Regan, 1907; and *Arius milberti* Valenciennes, 1840a. I have not examined type material.

Arius Valenciennes, 1840

Arius Valenciennes, 1840a: 53 (type species, *Pimelodus arius* Hamilton, 1822, by absolute tautonomy).

Ariodes Müller and Troschel, 1849: 6 (type species, *Bagrus (Ariodes) arenarius* Müller and Troschel, 1849, by subsequent designation by Bleeker 1863).

Pseudarius Bleeker, 1862: 8 (type species, *Pimelodus arius* Hamilton, 1822, by original designation).

Diagnosis. *Arius* is characterised by having single patches of granular (molariform, coarse, conical and usually blunt) teeth on each side of the palate, rakers present along the back of all gill arches, and the lateral line usually bifurcating at the tail base. In combination with these, the mesethmoid has a deep, median notch, the vomer is 'T'-shaped, the hind margin of the metapterygoid is aligned with the hind margin of the quadrate and the vomer is edentate.

The subvertebral cone is moderately to well-elevated and the laminae and ridges of the fourth neural spine and epioccipital are low to moderately elevated. The nasal bone is a simple, straight tube or curves in line with the mesethmoid neck, and the lachrimal has a well-produced angle. The mandibulary pores are moderately large or small (*A. manillensis*). The epioccipital does not enter the skull roof. The temporal fossa is prominent or tends to reduce with growth (*A. arius*) and the posterior cleithral process is often heavily ossified proximally. The skull surface is granular to rugose or striate, and the elongate posterior dorsomedian fontanelle reduces with ontogeny or remains. There are four infraorbitals. The frontal bone is moderately broad at its middle or posteriorly and the process of the lateral ethmoid becomes prominent in some species.

The gill opening is moderately wide to less wide and the buccopharyngeal pads are poorly to well developed. The chin barbel bases are evenly spaced (neither close together nor wide apart), the adipose fin base is moderately long, the lateral line usually bifurcates at the tail base (although in individuals of different species it may only turn upwards), the swim bladder is rounded or heart-shaped, the gonads are bilobate and mature females develop pads on the inner pelvic fin rays. Rakers are present along the back of all gill arches (sometimes absent from the first arch in *A. oetik*). The two palatal tooth patches are situated towards the front (e.g., *A. dispar*, *A. arenarius*, *A. arius*), more posteriorly (e.g., *A. maculatus*), lengthwise from front to back (e.g., *A. gagora*) or over much of the palate (*A. manillensis*).

Arius arius: Br 6. A. 17–22. P. 1,10–11. Total gill rakers (first arch) 14–17. Vertebrae 7+11–12+5+29, total 52–53.

All species: Br 6–7. A. 17–23. P. 1,10–12. Total gill rakers (first arch) 13–21. Vertebrae 6–8+11–13+4–6+27–30, total 49–54.

Comparisons. The palatal teeth of *Arius* are always granular, yet sometimes they have acute tips (e.g., *A. dispar*). In *A. microcephalus* they are large and globular. Individuals of *A. oetik* have a grey peritoneum (cf. *Hexanematichthys*), not common in the genus. Extra (posterior) patches of palatal teeth may be present (*A. dispar*). It is only in *Arius* and *Plicofollis* n. g. that brooding males shed palate teeth as a protection for the brooded young instead of, or as well as (e.g., *A. microcephalus*), enveloping the teeth in thickened palate epithelium (as is usual in other genera).

Distribution. The Andaman Islands and the east coast of India to Sumatra, Java and the Philippines. Coastal waters and estuaries and into freshwater (*A. jatius*, *A. manillensis*).

Taxa. More than thirty nominal species, of which the following are probably valid: *Arius arenarius* (Müller and Troschel, 1849) (synonyms: *Arius fangi* Chaux in Chaux and Fang, 1949; *Arius sinensis* Chu *et al.*, 1999 (non Lacépède)); *A. arius* (Hamilton, 1822) (synonyms: *Arius falcarius* Richardson, 1845; *Arius cochinchinensis* Günther, 1864; *Arius boakeii* Turner, 1867; ?*Arius buchanani* Day, 1877); *A. dispar* Herre, 1926; *A. gagora* (Hamilton, 1822); *A. jatius* (Hamilton, 1822); ?*A. jella* Day, 1877; *A. leptonotacanthus* Bleeker, 1849 (synonym: *Arius goniaspis* Herre, 1926 (non Bleeker)); ?*A. macracanthus* Günther, 1864; *A. maculatus* (Thunberg, 1792) (synonyms: *Pimelodus thunberg* Lacépède, 1803; *Arius gagoroides* Bleeker, 1846; *Arius pidada* Bleeker, 1846 (in part); *Arius arius* Bleeker, 1858 (non Hamilton); *Hemipimelodus bicolor* Fowler, 1935; *Hemipimelodus atripinnis* Fowler, 1937); *A. malabaricus* Day, 1877; *A. manillensis* Valenciennes, 1840a: 93 (synonym: *Pseudarius philippinus* Sauvage, 1880); *A. microcephalus* Bleeker, 1855 (synonym: *Arius sciurus* Smith, 1931); *A. oetik* Bleeker, 1846 (synonym: *Arius pidada* Bleeker, 1846 (in part)); *A. platystomus* Day, 1877; *A. sumatranus* (Bennett, 1830); *A. venosus* Valenciennes, 1840a.

Literature synonyms of *Arius falcarius* are *Bagrus crinalis* Richardson, 1846 and *Pimelodus mong* Richardson, 1846. Literature synonyms of *A. maculatus* are *A. sinensis* Valenciennes, 1840 (synonym: *Pimelodus tachisurus* Valenciennes, 1840a); *A. angulatus* Bleeker, 1846; *A. chondropterygioides* Bleeker, 1846; *A. heckelii* Bleeker, 1846 and *A. viviparus* Bleeker, 1846. Literature synonyms of *Arius venosus* are *A. laeviceps* Bleeker, 1846; *A. macruropterygius* Bleeker, 1846; *A. manjong* Bleeker, 1846; *A. micronotacanthus* Bleeker, 1846 and *A. micruropterygius* Bleeker, 1847. I have not examined type material of these taxa.

Comments. The relationship of the following taxa should be investigated: (1) *A. dispar* with *A. manillensis*; (2) *A. venosus* and *A. sumatranus* (Day (1877), followed by Kailola (1999) who remarked that the species are closely allied; they may be synonymous); (3) *A. jella*, *A. macracanthus* and *A. malabaricus* with *A. maculatus* and *A. gagora*. The type of *A. macracanthus* is from Siam: Smith (1945) followed Day's (1877) decision to include it in the synonymy of *A. gagora*. Hamilton (1822: 168) stated of *A. gagora*: 'On the palate are two bones covered with sharp crowded teeth', which raises the question of whether Day (1877: 465–466) and later authors (e.g., Jayaram 1982) were describing the same species (my material was from Day's collection). Dhanze and Jayaram (1982) recognised *A. gagora* and *A. jella*. *Arius gagora* has page priority over *A. arius* and is figured by Hamilton (1822: pl. 10, fig. 54).

Arius manillensis Valenciennes, 1840a: 93 (also in Herre 1926) is not conspecific with *Pimelodus* *manillensis* Valenciennes, 1840a (in Désoutter 1977 as *Hemipimelodus manillensis*). The status of *Pimelodus manillensis* is uncertain, as is that of *Hemipimelodus manillensis* of Day (1877), Chandy (1953) and Jayaram (1982).

Aspistor Jordan and Evermann, 1898

Aspistor Jordan and Evermann, 1898: 2763 (type species *Arius luniscutis* Valenciennes, 1840a, by original designation)

Diagnosis. *Aspistor* is characterised by the combination of a (usually) broad, granular or rugose head, the epioccipital usually invading the skull roof, a moderate to high subvertebral cone, a single (anterior chamber) swim bladder, elongate distal caudal vertebrae (sometimes), and 5–12 thoracic vertebrae.

The mesethmoid is shallowly notched anteriorly. The frontal bone is broad, expanding forwards with age to reduce the space between it and the lateral ethmoid, although in *A. kessleri* and *A. hardenbergi* the frontal arms are narrow and the space moderately large. The supraoccipital is either short and broad, or elongate, and the predorsal bone ('nuchal plate') increases in size with growth and becomes large (either butterfly-shaped or crescentic) in some species (e.g., *A. luniscutis*, *A. quadriscutis*). The laminae and ridges of the fourth neural spine and epioccipital are moderately or well-developed. The extrascapular remains as a distinct bone. The temporal fossa remains open (e.g., *A. planiceps, A. quadriscutis*) or is closed over (e.g., *A. platypogon, A. luniscutis*), the posterior dorsomedian fontanelle is reduced, and the mandibulary pores are either tiny or moderately large. The distal caudal vertebrae are noticeably elongate in some species. The post-cleithral process is broad and bears radiating lines of granules.

The teeth on the jaws are conical; bluntly conical or granular on the palate. The vomerine tooth patches coalesce to form one patch with age, the much larger and elongate autogenous patches on the palate expand with age, sometimes extending over most of the palate except for a narrow space along its midline, and parasphenoid /orbitosphenoid teeth are sometimes present (e.g., *A. platypogon*). The barbels are thick proximally and thin distally; the gill openings moderately wide, their margins free; rakers are absent from the back of the first and second gill arches. The dorsal and pectoral fin spines are robust and granular in front and serrated behind (strongly so in *A. kessleri*); the adipose fin base is long (*A. hardenbergi*) to short (*A. platypogon*). The swim bladder is rounded or heart-shaped and in *A. platypogon* there are low ridges along the inner pelvic fin rays. The condition of the pelvic fins in mature females is unknown. In juvenile(?) *A. platypogon* the buccal cavity and gill arches may be charcoal or dusky, and in this species and *A. hardenbergi* the upper aspects of the paired fins are often dark blue.

Aspistor luniscutis: Br? A.18–20. P. I,11. Total gill rakers (first arch) 12–14. Vertebrae – (not available).

All species: Br 6?. A. 16–20. P. I,9–11. Total gill rakers (first arch) 10–15. Vertebrae 7–8+5–12+5–8+26–32, total 49–55.

Comparisons. *Aspistor*, *Sciades* and *Hexanematichthys* are closely related taxa and share a comparable morphology. Their most striking characters are the broad, granular head (though not in all species), expansive frontal bone and the expanding predorsal plate (not in all species). *Aspistor* is distinguished however, by the combination of high subvertebral cone (moderately low in the other taxa), the epioccipital invading the skull roof in most taxa while the extrascapular remains as a distinct bone (in *Sciades emphysetus* and *S. proops* the epioccipital nudges the skull roof), the notched mesethmoid with two diverging, curved cornuae, the simple, rod-like nasal bone, a low number (5–12) of thoracic vertebrae (cf. 11–20 in *Sciades*, 13–18 in *Hexanematichthys*), a single (anterior chamber) swim bladder (cf. *Sciades*) and a lower gill raker count (11–15 cf. 16–24 in *Sciades*, 12–18 in *Hexanematichthys*). *Bagre marinus* and *Plicofollis* n. gen. species have elongated distal caudal vertebrae also, but the elongation is vertical rather than horizontal (as here).

Distribution. North-eastern South America, western central America, southern New Guinea. Inshore coastal waters and estuaries.

Taxa. Seven to eleven valid species: ?*Aspistor cookei* (Acero and Betancur-R, 2002); *A. hardenbergi* (Kailola, 2000); *A. kessleri* (Steindachner, 1877) (synonyms: *Arius elatturus* Jordan and Gilbert, 1883; *Netuma insularum* Greene in Gilbert, 1897); *A. luniscutis* (Valenciennes, 1840a); ?*A. neogranatensis* (Acero and Betancur-R 2002a); ?*A. osculus* (Jordan and Gilbert, 1883); *A. planiceps* (Steindachner, 1877); *A. platypogon* (Günther, 1864) (synonym: *Netuma mazatlana* Gilbert, 1904); *A. quadriscutis* (Valenciennes, 1840a), ?'*Arius*' species A of Kailola and Bussing, 1995 and ?'*Arius*' species B of Kailola and Bussing, 1995.

Comments. The studies by Aguilera and de Aguilera (2004) and Acero and Betancur-R (2002, 2002a) aided my determination of this genus.

Bagre Cloquet, 1816

Bagre Cloquet, 1816: 52 (type species *Silurus bagre* Linnaeus, 1766, by absolute tautonomy).

Glanis Agassiz in Spix and Agassiz, 1829: 46 (type species *Silurus bagre* Linnaeus, 1766, by subsequent designation by Kottelat 1988).

Stearopterus Minding, 1832: 116 (type species *Stearopterus bagre* Minding, 1832, by monotypy).

Breviceps Swainson, 1838: 328, 343 (type *Silurus bagre* Bloch, 1794, by monotypy. Name preoccupied; replaced by *Felichthys* Swainson, 1839).

Ailurichthys Baird and Girard, 1854: 26 (type species *Silurus marinus* Mitchill, 1815, by subsequent designation by Jordan and Evermann 1896. Spelled *Aelurichthys* by Gill 1863).

Mystus Gronow in Gray, 1854: 155 (type species *Mystus carolinensis* Gray, 1854, by subsequent designation by Jordan and Evermann 1896).

Auemanotus Fowler, 1944: 171 (type species *Ailurichthys panamensis* Gill, 1863, by original designation).

Diagnosis. *Bagre* is characterised by having two pairs (maxillary and mental) of barbels of which the maxillary barbels are long and strap-like; the pectoral, and sometimes the dorsal spine, bearing a long, strap-like and striated filament; three forward extensions from each side of the frontals; thin cranial bones, tending to be vacuolated; a low and flat subvertebral cone; and many (19–36) anal fin rays.

The usually convex mesethmoid has broad cornuae, the nasal bone is either curved or irregularly shaped (*B. bagre*) and there are three (*B. bagre*) to six (*B. marinus*) infraorbitals. The frontals are broad, humped, expanding anteriorly with growth. The three arms directed anteriorly interface with the mesethmoid and the lateral ethmoid. The frontal also bears two longitudinal ridges or rods aligned with the nasal bones (ridges covered by a shelf of vacuolated bone in *B. marinus*); and the frontal-lateral ethmoid space is much reduced or absent. The ovate posterior dorsomedian fontanelle reduces with growth. The epioccipital invades the skull roof (*B. marinus, B. bagre*) as an additional skull bone, that portion matching in ornamentation the other dermal bones. The laminae of the laterally expanded fourth neural spine and epioccipital are moderately to well elevated, yet the lamina bone itself is thin. The superficial bone covering the fused vertebrae is either flat or keeled medially (*B. panamensis*, *B. marinus*) and excavated posteriorly, and may be lacking anteriorly (*B. marinus*). The first pharyngobranchial is situated distally. The metapterygoid hind margin is either in line with the hind margin of the quadrate (*B. panamensis*) or well behind it. There are 5–6 large or 7–8 small mandibulary pores. In *Bagre marinus* the posterior vertebrae are vertically extended.

The cranial dorsal surface is smooth. The lips are thin or absent, except at the mouth corners, and the teeth are villiform or pointed and conical: they form bands on the jaws and the two vomer and two palatal patches. The mental barbel bases are aligned; the gill membranes are free; rakers are absent from the back of the first gill arch and either present or absent from the back of the second arch; and low buccopharyngeal pads and pocket are present. The adipose fin is short-based and situated posteriorly and the lateral line bifurcates at the tail base. The posterior cleithral process is short, and the fin spines are moderately thin and finely serrated. The condition of the pelvic fins in mature females is unknown.

Bagre bagre: Br 6. A. 30–36. P. I,13. Total gill rakers (first arch) 8–10. Vertebrae 6+12+7+33, total 58.

All species: Br 6. A 19–36. P. I,11–13. Total gill rakers (first arch) 8–21. Vertebrae 6–7+9–14+6–8+29–37, total 55–61.

Comparisons. The high anal fin ray count of *Bagre* compares only with *Nedystoma novaeguineae* and *Cathorops hypophthalmus* and is a derived condition. Invasion of the skull roof by the epioccipital is a sporadic phenomenon in the Ariidae (see comment under *Cathorops*). Thinning of the skull bones is a derived condition; and the expansive laminae and plates of the fourth neural spine and epioccipital and the shelving coracoid appear to compensate *Bagre* for any loss of strength in its thin skull bones. In *Cinetodus froggatti* and *C. carinatus* the expanded fourth neural spine laminae and epioccipital lamina form a broad transverse plate, as in *Bagre*. The shelf of the coracoid (pectoral girdle) is expanded and the symphysis wide (as in *Brustiarius*). Weak cranial ossification occurs also in *Nedystoma novaeguineae* and, possibly, *Brustiarius nox*. Honeycomb-textured or 'porous' bones (frontal bones in *Bagre*) also occur in *Plicofollis* n.gen. *dussumieri*, *Plicofollis* n.gen. *nella*, *Osteogeneiosus* and possibly *Hemiarius grandicassis* (lateral ethmoid expansion; supraoccipital process) and *Sciades* species (predorsal plate). As well as in *Bagre*, a much expanded frontal bone occurs in older individuals of *Netuma bilineatus*, *Hexanematichthys mastersi*, *Sciades* and some *Aspistor* species. Some *Plicofollis* n.gen. species also possess vertically extended vertebrae. The metapterygoid in *B. marinus* is high and expanded and its suture with the hyomandibular is narrow.

Distribution. South-eastern North America, eastern and western coasts of Central America, north-eastern South America, north-western South America. Inshore marine to fresh water (*B. marinus*).

Taxa. Four valid species: *Bagre bagre* (Linnaeus, 1766); *B. marinus* (Mitchill, 1815); *B. panamensis* (Gill, 1863) (synonyms: *Aelurichthys nuchalis* Günther, 1864; *Aelurichthys scutatus* Regan, 1907); *B. pinnimaculatus* (Steindachner, 1877) (synonym: *Galeichthys eydouxii* Valenciennes, 1840a).

A literature synonym of *B. bagre* is *Felichthys filamentosus* Swainston, 1839 (Marceniuk and Ferraris 2003), and a literature synonym of *B. panamensis* is *Aelurichthys isthmensis* Regan, 1907 (Marceniuk and Ferraris Jr 2003).

Batrachocephalus Bleeker, 1846

Batrachocephalus Bleeker, 1846: 176 (type species *Batrachocephalus ageneiosus* Bleeker, 1846, by monotypy).

Diagnosis. *Batrachocephalus* is characterised by having fixed teeth, edentate vomer, bifurcate lateral line, thick fin spines, convex mesethmoid, reduced skull fossae, a deeply excavated laminar bone over the anterior fused vertebrae and one pair of (mandibulary) barbels.

The neurocranium is smooth anteriorly and rugose to granular posteriorly. *Batrachocephalus mino* has exceedingly strong jaws, a prominent lower jaw, and the cranial bones are strong, heavy and thick. The nasal bone is expanded and irregularly shaped and the lachrimal is almost rectangular. The vomer is 'T'-shaped. The ridges and laminae of the neural spine and epioccipital are low. The deep excavation of the laminar bone on the anterior fused vertebrae exposes the bases of some transverse processes; and the laminar bones bears a high and acute median keel. The frontals are broad posteriorly. The extrascapular is distinct. The metapterygoid hind margin lies slightly beyond the hind margin of the quadrate; and the large metapterygoid extends well forward – almost to the front of the vomer and lateral ethmoid. The metapterygoid-hyomandibular suture is broad. The first pharyngobranchial is short and lies near the epibranchial angle.

The head is rounded and the snout is blunt. The mouth gape is wide (40–45% of head length), extending to below the large eyes which are placed well forward. The mandibulary barbels are short, reaching only to the eye. The jaw teeth are peg-like with blunt tips and the jaw bands are often edentate mesially. The palatal teeth are conical and blunt tipped, in a broad, short longitudinal band on each side of palate, close to the jaw teeth. The gill rakers are 'club'-shaped and rakers are present along the back of all gill arches; the buccopharyngeal pads are poorly developed. The posterior cleithral process is rugose and heavily ossified anteroventrally. The fin spines are strong: flattened with dentae along both borders. The swim bladder is almost triangular and its sides are smooth. The gonads are bilobed. The condition of the pelvic fin in mature females is unknown.

Br 5. A 19–22. P. I,8–9. Total gill rakers (first arch) 15. Vertebrae 7+10+5+28, total 50.

Comparisons. Club-shaped gill rakers are present in *Cinetodus froggatti*, and broad outer branchiostegal rays occur also in *Ketengus, Plicofollis* n.gen. and *Cathorops*. The strongly ossified head and heavy jaws of *B. mino* are homologous with those of *Ketengus* and *Osteogeneiosus*.

In my study, the PAUP analyses consistently paired *Batrachocephalus mino* with *Cryptarius* n.g. *truncatus*, isolating them from the phenotypically similar taxa *Amissidens hainesi, Osteogeneiosus militaris* and *Ketengus typus* (see *Cryptarius* n. gen. for comment).

Distribution. South-east Asia from India to Burma, Thailand, Malaya, Sumatra, Borneo and Java. Coastal waters to lower reaches of rivers.

Taxa. The only valid member of this genus is *Batrachocephalus mino* (Hamilton, 1822).

Literature synonyms of *B. mino* are *Batrachocephalus ageneiosus* Bleeker, 1846 and *Bagrus micropogon* Bleeker, 1858, but the latter species has been shown to be a bagrid catfish, *Leiocassis micropogon* (Bleeker) (Roberts 1989; Kottelat *et al.* 1993; Tan and Ng 2000). I have not examined type material of *B. ageneiosus*.

Brustiarius Herre, 1935

Brustiarius Herre, 1935: 388 (type species *Arius nox* Herre, 1935, by original designation).

Diagnosis. *Brustiarius* is easily identified by the combination of its large eyes (4–7% SL), thin jaws, upturned jaw symphyses and terminal mouth, thin barbels rounded in cross section, slender and deeply-forked caudal fin, few (8–10) pectoral fin rays, many (19–67) rakers on the first gill arch, the small adipose fin, and the slender uncinate process of the third epibranchial articulating with the fourth epibranchial.

The neurocranium is thin, the temporal fossa is absent and the posterior dorsomedian fontanelle tends to reduce in size with growth. The subvertebral cone is moderately elevated. The metapterygoid is enlarged and situated posteriorly in relation to the quadrate and the suture between it and the hyomandibular bone is short.

The skull is smooth to slightly rugose. The head is depressed and the snout is rounded; the teeth are small and curved: in few series in the jaws and in four patches on the palate (two vomerine, two autogenous), which are often confluent, sometimes butterfly-shaped, sometimes united into a large square covering most of the palate; or palate sometimes devoid of teeth. Rakers are usually absent from the back of the first two gill arches (sometimes there are a few) and large buccopharyngeal pads are present (*B. nox*) or not (*B. solidus*). The gill openings are wide. The posterior cleithral process is either very short (*B. nox*) or moderately long (*B. solidus*), but always acute. The fin spines are thin and bear fine serrae (*B. nox*) or are of moderate size (*B. solidus*). The adipose fin is situated over the posterior of the anal fin and the swim bladder is almost rounded. The buccopharyngeal cavity is dark in *B. nox*, and the peritoneum (both species) is dusky. Pads are present on the pelvic fins of mature females.

Brustiarius nox: Br 6. A. 18–21. P. I,8–9. Total gill rakers (first arch) 56–67. Vertebrae 6–7+10–11+5–8+29–31, total 51–53.

All species: Br 6. A. 17–23. P. I,8–10. Total gill rakers (first arch) 19–67. Vertebrae 6–7+9–13+5–8+29–30, total 51–56.

Comparisons. *Brustiarius* exhibits a trend towards reduced cranial ossification, including its thin jaws. The pectoral girdle is also thin and shelving (although the symphysis between the two coracoid bones is exceptionally broad). Weak cranial ossification and/or a thin premaxillary occurs in *Nedystoma, Bagre, Cephalocassis* and *Amissidens hainesi.* Other taxa possessing a narrow hyomandibular-metapterygoid suture include *Hemiarius dioctes*, cf. *Arius macrorhynchus, Cephalocassis melanochir, Plicofollis* n. gen. *nella* and *P.* n. gen. *polystaphylodon. Brustiarius* shares with *Nedystoma* the character state of a urohyal with slender arms tending to bifurcate distally. A dark buccopharyngeal cavity occurs in juveniles of the central American taxon *Aspistor platypogon* as well as in some *Amissidens hainesi* individuals.

A character difficult to quantify is noticeable in *Brustiarius*: a long facet indicating the contact area between the palatine bone and the lateral ethmoid (also present in *Plicofollis* n.gen. and *Nedystoma dayi*).

Distribution. Northern New Guinea. Freshwater.

Taxa. Two valid species: *Brustiarius nox* (Herre, 1935); *B. solidus* (Herre, 1935) (synonyms: *Arius kanganamanensis* Herre, 1935; *Hemipimelodus bernhardi* Nichols, 1940; *Arius microstomus* Nichols, 1940).

Cathorops Jordan and Gilbert, 1883

Cathorops Jordan and Gilbert, 1883: 39, 54 (type species *Arius hypophthalmus* Steindachner, 1877, by original designation; also by monotypy).

Diagnosis. *Cathorops* is distinguished by the ventral aorta and jugular veins lying together, ventral to the vertebral centra; the strongly elevated subvertebral cone; the very high transverse lamina of the fourth neural spine; the epioccipital invading the skull roof; a toothless vomer; and rakers lying along the back of all gill arches.

In some taxa the nasal bone is irregularly shaped (almost straight in others). The frontal bone is broad posteriorly with narrow anterior arms and the ventral shaft of the neurocranium is notably narrow. The posterior dorsomedian fontanelle is very small or absent (even in juveniles). The second to fifth transverse parapophyses are angled at a right angle or forward, the posterior margin of the laminar bone over the anterior vertebrae is truncate or convex and raised distally, and the high subvertebral cone is often notched at its anterior base. The posteromedian flange of the epioccipital is high and abuts the lamina of the fourth neural spine. The epioccipital in the skull roof is amalgamated with the extrascapular, that portion matching in ornamentation the other dermal bones; the temporal fossa is much reduced or absent (adults). The metapterygoid is situated posteriorly, its hind margin in line with or beyond the hind margin of the quadrate. The first branchiostegal ray is exceptionally broad, and the mandibulary pores are large or small. The postcleithral process is very short.

The jaw teeth are fine and sharp, except in some species where the teeth in the inner row on the mandible are molariform. The teeth on the palate are conical to molariform and in two patches. The eye of *C. hypophthalmus* is situated below the level of the mouth angle and lacks a free orbital rim; in other species the eye is dorsolateral and has a free orbital margin. The dorsomedian fontanelle is groove-like posteriorly; the head shield is rough to striate, the sides and top of the head are often venulose. Usually the gill openings are restricted and the membranes are not free across the isthmus (gill openings not restricted in *C. dasycephalus*, and wide with free margins in *C. hypophthalmus*). In some species there are two rows of rakers along the back of the anterior gill arches, and buccopharyngeal pads and flaps are well-developed in some species. The chin barbels are staggered. In *C. hypophthalmus* the barbels are long and rounded in cross section; barbels moderately flattened in other species. Usually the adipose fin is short-based and situated over the posterior third of the anal fin. The gonads are bilobate and pads (in some species expressed as a curious double thickening) are present on the inner pelvic fins of mature females.

Cathorops hypophthalmus: Br 6. A. 21–23. P. I, 10–11. Total gill rakers (first arch) 37–41. Vertebrae – not available.

All species: Br 6. A. 19–28. P. I,10–11. Total gill rakers (first arch) 9–41. Vertebrae 6+7–10+ 3–5+26–32, total 43–52.

According to H. Higuchi (pers. comm.), the males of some taxa lose gill rakers when brooding.

Comparisons. In most other ariids, each jugular vein lies lateral to the centra of the vertebral column. *Cathorops* is most closely related to *Potamarius* and several Indo-Australian genera. For example, in *Potamarius* the parapophyses of the fifth and sixth vertebrae are united, and angled forward also. Only *Cinetodus* and *Cathorops* possess a united extrascapular + epioccipital: in several other taxa the epioccipital invades the skull roof (e.g., some species of *Plicofollis* n. gen. *Netuma proximus, Hemiarius sona, Bagre marinus, Aspistor* species and *Cryptarius* n. gen. *truncatus*) but in them the extrascapular remains as a distinct bone. The exceptionally broad first branchiostegal ray is a character shared with the South-east Asian taxa *Ketengus, Plicofollis* n. gen. and *Batrachocephalus.* The urohyal is broad and truncate anteriorly (also in *Cephalocassis*). *Cathorops* and

Nedystoma species have low numbers of thoracic (7–10) and haemal (2–6) vertebrae.

Distribution. Eastern and western Central America; north-eastern South America. Inshore coastal waters, estuaries and lower reaches of rivers, also freshwater.

Taxa. More than twenty nominal species, of which Marceniuk and Ferraris Jr (2003) considered the following as valid: *Cathorops agassizii* (Eigenmann and Eigenmann, 1888); *C. aquadulce* (Meek, 1904); *C. arenatus* (Valenciennes, 1840a); *C. dasycephalus* (Günther, 1864) (synonym: *Tachisurus longicephalus* Eigenmann and Eigenmann, 1888); *C. fuerthii* (Steindachner, 1877) (synonyms: *Tachysurus liropus* Bristol in Gilbert, 1897; *Tachysurus evermanni* Gilbert and Starks, 1904); *C. hypophthalmus* (Steindachner, 1877) (synonym: *Tachisurus gulosus* Eigenmann and Eigenmann, 1888); *C. melanopus* (Günther, 1864); *C. multiradiatus* (Günther, 1864) (synonyms: *Bagrus arioides* Kner, 1863; *Tachysurus emmelane* Gilbert in Jordan and Evermann, 1898; *Tachysurus equatorialis* Starks, 1906); *C. spixii* (Agassiz in Spix and Agassiz, 1829) (synonym: *Pimelodus albidus* Agassiz in Spix and Agassiz, 1829); *C. steindachneri* (Gilbert and Starks, 1904) (synonym: *Arius taylori* Hildebrand, 1925); *C. tuyra* (Meek and Hildebrand, 1923).

Cephalocassis Bleeker, 1857

Cephalocassis Bleeker, 1857: 473 (type species *Arius melanochir* Bleeker, 1852, by subsequent designation by Bleeker 1862).

Hemipimelodus Bleeker, 1857: 473 (type species *Pimelodus borneensis* Bleeker, 1851, by monotypy.

Diagnosis. *Cephalocassis* is characterised by the combination of small and conical jaw teeth; the eyes covered (*C. borneensis*) or partly covered (*C. melanochir*) by skin; the mouth small and nape high; the gill openings restricted and the adipose fin long-based. The buccopharyngeal pads and flaps are well-developed, and the chin barbel bases are close together and aligned. The posterior dorsomedian fontanelle is heart-shaped or triangular, and is open at all growth stadia. The pterotic bone is thin and cartilaginous anterodorsally, creating a depression in the cranium between the supraoccipital and the sphenotic. The subvertebral cone is strong and high, the epioccipital just invades the skull roof adjacent to the extrascapular, the supraoccipital process is narrow and long, and the posterior cleithral process is short and heavily ossified anteroventrally.

The neurocranium is slightly rugose or striate or smooth. The posterior dorsomedian fontanelle is open at all growth stadia. The temporal fossa is very small or absent, the supracleithrum depressed at its position. The metapterygoid hind margin aligns with the hind margin of the quadrate, and the suture between it and the hyomandibular is short. The vomer is wedge-shaped, the frontals are broad posteriorly with long anterior arms, and the laminar bone over the anterior fused vertebrae is extensive and only shallowly excavated medially. There are five (*C. melanochir*) or four infraorbital bones. In *C. borneensis*, the fifth and sixth pelvic fin rays bear noticeable dentae (ridges) along their length (possibly only in females).

The mouth is subterminal and the snout is somewhat conical. The palate is edentate (*C. borneensis*) or possesses a small autogenous patch of sharp-tipped conical teeth on each side (*C. melanochir*). In *C. melanochir*, where rakers are usually absent from the back of the first two gill arches, they are replaced by double rows of many large papillae; in *C. borneensis* rakers are always present along the back of the gill arches. The fin spines are flat, robust and strongly serrated (less strong in *C. borneensis*) and chambered (*C. melanochir*). The lateral line turns upwards (*C. melanochir*) or usually bifurcates at the tail base (*C. borneensis*). The swim bladder is rounded, pads develop on the inner pelvic fin rays of mature females and the gonad in females appears to be bilobate. The upper surface of the pectoral and pelvic fins are often coloured dark bluish-brown.

Cephalocassis melanochir: Br 6. A. 17–19. P. I,10–11. Total gill rakers (first arch) 12–15. Vertebrae 6+13+3+30–31, total 52–53.

All species: Br 5–6. A. 16–19. P. I,9–11. Total gill rakers (first arch) 12–18. Vertebrae 5–6+9–13+3–5+27–31, total 46–53.

Comparisons. As with other ariid genera, homoplasies abound. *Cephalocassis* is superficially similar to *Cinetodus* but pads develop on the inner pelvic fin rays of mature females (not in *Cinetodus*), the epioccipital just enters the skull roof (not in *Cinetodus*), the extrascapular and the epioccipital are not combined (as they are in *Cinetodus*) and the laminae of the epioccipital and the fourth neural spine are not much elevated (well elevated in *Cinetodus*). The lateral line is ramose with extensive smaller lines (especially over the shoulder), a feature also present in, for example, *Cinetodus, Hemiarius dioctes, H. stormii* and *Cryptarius* n. gen.. The shape of the urohyal is identical to that of *Ketengus* and *Cathorops*. Chambered fin spines are shared by some species of *Hemiarius, Plicofollis* n. gen. *Cryptarius* n. gen. *truncatus, Nemapteryx nenga, N. macronotacanthus* and *Netuma thalassinus*. The configuration of the dorsomedian fontanelle is similar to that of *Nedystoma dayi*, a (partially) concealed eye is characteristic also of *Hemiarius insidiator, Nedystoma novaeguineae* and *Cathorops hypophthalmus*, and ridged inner pelvic fin rays are also present in *Cryptarius* n. gen. *truncatus* and *Aspistor platypogon*. The wedge-shaped vomer is shared with *Cryptarius* n. gen. *truncatus*.

Distribution. South-east Asia (Thailand, Vietnam and Cambodia, Sumatra, Borneo). In rivers; freshwater.

Taxa. Two valid species: *Cephalocassis borneensis* (Bleeker, 1851) (synonyms: *Arius macrocephalus* Bleeker, 1858 (non Bleeker, 1846); *Hemipimelodus siamensis* Sauvage, 1878; possible synonym: *Hemipimelodus intermedius* Vinciguerra, 1881); *C. melanochir* (Bleeker, 1852) (possible synonym: *Arius doriae* Vinciguerra, 1881).

Comments. The only stated difference between *Hemipimelodus intermedius* and *C. borneensis* is relative eye size (Weber and de Beaufort 1913; Désoutter 1977). Roberts (1989) provides good illustrations of both *C. borneensis* and *C. melanochir.* Literature descriptions (Smith 1945; Désoutter 1977) of *Hemipimelodus siamensis* do not record any difference between that taxon and *C. borneensis* and Kottelat (1984) placed *H. siamensis* in the synonymy of *C. borneensis.*

The suggested synonymy of *Arius doriae* is based on Heok Hee Ng's advice (pers. comm.) after he examined a 112 mm SL syntype (RMNH 10889).

Cinetodus Ogilby, 1898

Cinetodus Ogilby, 1898: 32 (type species *Arius froggatti* Ramsay and Ogilby, 1886, by original designation).

Pachyula Ogilby, 1898: 33 (type species *Hemipimelodus crassilabris* Ramsay and Ogilby, 1886, by original designation).

Tetranesodon Weber, 1913: 545 (type species *Tetranesodon conorhynchus* Weber, 1913, by monotypy).

Septobranchus Hardenberg, 1941: 223 (type species *Septobranchus johannae* Hardenberg, 1941, by monotypy.

Diagnosis. *Cinetodus* is characterised by the combination of conical head, broadly triangular supraoccipital process, a small (16–35% HL) inferior mouth, a restricted gill opening, a long, horizontal and oblong posterior cleithral process, high and strong subvertebral cone, the proximal dorsal aspect of the pectoral fins dark blue or black in colour, mature females lacking thickened pads on the inner pelvic fin rays, a long-based adipose fin, and rakers present along the back of all gill arches.

The skull is strongly ossified and the rear of the skull is strengthened by the well-elevated and extensive laminae of the fourth neural spine and the ventral aspect of the supraoccipital, and the strong and compact pectoral girdle and high coracoid keel. The lateral ridge of the fourth neural spines is high, extending half-way up the neural spine, the posteromedian flange of the epioccipital abuts this ridge and is very well-elevated, and a median flange extends from the ventral surface of the supraoccipital (*C. froggatti, C. carinatus*). The extrascapular and epioccipital are amalgamated to form one unit in the skull roof. The rectangular posterior dorsomedian fontanelle is either always open (*C. crassilabris*) or reduces in size during growth. However, the temporal fossa is large and remains so, and the frontal bones are broader posteriorly with long anterior arms and a large lateral ethmoid-frontal space. The mandibulary pores are large. The Mullerian ramus is long. In *C. crassilabris* and *C. conorhynchus* the first pharyngobranchial is present (lost or fused with the epibranchial in the other species).

Cinetodus species have a high nape, and striate or smooth upper head surface. The lips are often fleshy and thick, and the chin barbel bases are close together and transversely aligned. The palate is either edentate (*C. crassilabris, C. conorhynchus*), bearing autogenous palatal tooth patches only (*C. froggatti*) or bearing vomer and palatal tooth patches (*C. carinatus*). The long-based adipose fin spans all of the anal fin. The pectoral axillary pore is large. In *C. crassilabris* and *C. conorhynchus* the back of the gill arches bear numerous papillae (smooth in the other species).

Cinetodus froggatti: Br 5. A. 17–19. P I,10–11. Total gill rakers (first arch) 11–16. Vertebrae 6–7+11–12+4+29–30, total 49–52.

All species: Br 5–6. A. 15–19. P. I,9–11. Total gill rakers (first arch) 11–19. Vertebrae total 44–54.

Comparisons. Additional character states in *Cinetodus froggatti* are depressions in the laminar shelf of the anterior fused vertebrae (also in *Nedystoma dayi, Guiritinga barbus*), and the anterior sensory tubules of the lateral line being surrounded by thin bony plates (also in *Hexanematichthys*). *Cinetodus crassilabris* also possesses a uniquely shaped urohyal (broad and truncate anteriorly), and the parhypural of the caudal skeleton is clearly sutured with hypurals 1 + 2 (also in some *Plicofollis* n. gen. and *Netuma* species). Phylogenetic analyses indicated a close relationship between *Cathorops* and *C. crassilabris* based on the highly developed flanges at the back of the neurocranium and the well-developed and intrusive epioccipital. The Mullerian ramus appears to be longer in *Cinetodus* (and *Hemiarius stormii, Amissidens hainesi* and *Nedystoma dayi*) than in many other ariid taxa.

Distribution. Sahul Shelf (southern New Guinea and northern Australia). Mainly freshwater; *C. froggatti* also into estuaries and coastal waters.

Taxa. Four (perhaps three) valid species: *Cinetodus carinatus* (Weber, 1913); *C. crassilabris* (Ramsay and Ogilby, 1886); *C. conorhynchus* (Weber, 1913) (known only from the type); *C. froggatti* (Ramsay and Ogilby, 1886) (synonym: *Septobranchus johannae* Hardenberg, 1941).

Cochlefelis Whitley, 1941

Cochlefelis Whitley, 1941: 8 (type species, *Arius spatula* Ramsay and Ogilby, 1886, by original designation).

Diagnosis. *Cochlefelis* species are characterised by their long and depressed head and their broad, curved upper jaw extending well forward of the lower jaw such that the broad bands of upper jaw teeth are exposed; the long-based adipose fin; concave ventral aspect of the mesethmoid; tiny mandibulary pores; and many (32–36) caudal vertebrae.

The head surface is slightly rugose or striate, mainly posteriorly. The mesethmoid has broad cornuae and the anterior margin is only slightly excavated. The temporal fossa is large at all ages, or reducing with age (*C. burmanicus*) and the posterior dorsomedian fontanelle is extensive, always open, and elongate. In *C. burmanicus* the frontal bones are broad posteriorly and have long anterior arms; in the other species they are narrower posteriorly with shorter arms and the very extensive lateral ethmoid obscures the space between the frontal arms. The posterior cleithral process is moderately long and acute and the pectoral girdle is thin and shallowly curved.

The teeth are conical, their tips acute or flattened or spatulate. On the palate there are vomerine and large palatal tooth patches (*C. danielsi, C. spatula*) or two small patches of palatal teeth. The series of jaw teeth increase in number as the fish ages (to more than 15 series). Rakers are present (*C. burmanicus*) or are not (*C. spatula, C. danielsi*) along the back of the first two gill arches; in *C. burmanicus* those on the first arch are few. The palate is smooth with barely developed buccopharyngeal flaps and pads. The barbels are strap-like or rounded (in *C. spatula* with a membranous inner margin), the maxillary or mandibulary pair the longest (perhaps reaching as far as the dorsal fin origin), and the bases of the chin barbels are very widely separated. The adipose fin is long-based, spanning much of the anal fin. The gill openings are wide and the pectoral axillary pore is tiny. The lateral line turns up at the tail base (sometimes bifurcates in *C. burmanicus*) and pads are present on the inner pelvic fin rays of mature females.

Cochlefelis spatula: Br 6. A. 20–23. P. I,11–12. Total gill rakers (first arch) 15–17. Vertebrae 6–7+12–13+6–7+33, total 56–59.

All species: Br 6. A. 19–27. P. I,10–12. Total gill rakers (first arch) 15–24. Vertebrae: 6?+13–14+5–7+32–36, total 53–61.

Comparisons. *Potamarius nelsoni* also has membranous inner margins to the barbels. Tiny mandibulary pores are characteristic of *Cinetodus*, *Ketengus* and *Cryptarius* n. gen. *truncatus*, and *Cinetodus* species, *Aspistor hardenbergi* and *Cephalocassis* also have a long-based adipose fin. Widely-separated bases of the chin barbels occur in several other taxa, including *Nemapteryx armiger*, *N. augustus*, *Nedystoma novaeguineae* and species of *Hemiarius*. However, only some species of *Bagre* and *Sciades* have more caudal vertebrae.

Distribution. South-east Asia (Burma, one species) and southern New Guinea. Freshwater (*C. spatula*) or tidal reaches of rivers and estuaries.

Taxa. Three valid species: *Cochlefelis burmanicus* (Day, 1870); *C. danielsi* (Regan, 1908); *C. spatula* (Ramsay and Ogilby, 1886) (synonym: *Arius (Hemiarius) nudidens* Weber, 1913); possibly more.

Comments. Day (1877) recorded that the eye of *C. burmanicus* is without a free margin but I do not find that in material I examined.

Cryptarius new genus

Type species: *Arius truncatus* Valenciennes, 1840a: 64, by original designation.

Diagnosis. *Cryptarius* is characterised by the combination of a restricted gill opening, small patches of teeth on the sides of the palate and absence of vomerine teeth, tiny mandibulary pores, a laminar shield that is deeply excavated medially such that the bases of some vertebral transverse processes are exposed, a wedge-shaped vomer, the epioccipital invading the skull roof as an additional bone (the exoccipital remaining distinct) and the female gonads united along their proximal third. The metapterygoid-hyomandibular suture is broad and the first pharyngobranchial is short and united with the epibranchial at its angle.

The neurocranium is smooth anteriorly and rugose to granular posteriorly. The mesethmoid is convex and the nasal bones are simple. The frontals are broad posteriorly and the ridges and laminae of the neural spine and epioccipital are low. The temporal fossa is reduced in size and the dorsomedian fontanelle is shallow. The metapterygoid hind margin lies above the middle of the quadrate.

There are three pairs of thin and short barbels and the bases of the chin barbels are close together and transversely aligned. The head is long and depressed with venulose sides, the small eye is placed low, the mouth gape is moderately small. The lips are thin and crenulate, and the jaw teeth are long and slender with curved tips. The anterior nostril lies directly in front of the posterior nostril. The gill opening is closed across the isthmus from just below the pectoral fin base, although the margin of the gill cover is free. In *C. truncatus* the upper insertion of the operculum is straight and not turned forward (as in most other ariids). Rakers are present along the back of all gill arches (sometimes few or none on the first two arches). The supraoccipital process is oblong and straight-sided. The fin spines are broad and long, serrated or granular along their posterior margin. In larger *C. truncatus* they are half-chambered. The posterior cleithral process is rugose and heavily ossified anteroventrally. The lateral line is ramose, especially anteriorly, the venules extending over the shoulder and sides of the head. The line is bifurcate at the tail base. The swim bladder is heart-shaped or triangular and is often scalloped on its exterior margin. The inner pelvic fin rays are ridged (?females only) and the caudal fin lobes are somewhat broad and 'paddle'-shaped.

Br 6–7. A. 20–25. P. I,8–11. Total gill rakers (first arch) 8–9. Vertebrae 7+11–13+4+29–31, total 50–55.

Etymology. From *kryptos* (Greek) meaning hidden or secret (Brown 1956) in reference to the unique combination of characteristics in this taxon having been ignored for such a long time.

Comparisons. Character states common to *Cryptarius* and *Batrachocephalus* include the edentate vomer, fixed jaw teeth, bifurcate lateral line at the tail base, broad fin spines, reduced skull fossae, convex mesethmoid and deeply excavated laminar bone. However, the differences between the taxa are significant: *B. mino* has one pair of barbels (three pairs in *C. truncatus*), the nasal and lachrimal bones are rectangular and uniquely shaped (simple in *C. truncatus*), the vomer is 'T'-shaped (wedge-shaped in *C. truncatus*), the epioccipital does not invade the skull roof, and the head and jaw bones are strongly ossified (thin or moderate in *C. truncatus*).

A reduced/united pharyngobranchial is present also in *Cinetodus*, proximally united gonads are present in *Amissidens hainesi*, *Cephalocassis melanochir* also has a wedge-shaped vomer, ridged inner pelvic fin rays are present in *Cephalocassis borneensis* and *Aspistor platypogon*, (half)-chambered fin spines are shared with *Netuma thalassinus*, some *Plicofollis* n. gen. and some *Nemapteryx* and *Hemiarius* species, and *Cephalocassis melanochir*, and species including *Nemapteryx armiger*, *Cephalocassis*, *Hemiarius*, *Osteogeneiosus*, *Bagre bagre*, *Cochlefelis burmanicus* and *Cathorops fuerthii* share a highly ramified lateral line. Tiny mandibulary pores are characteristic of members of *Cinetodus*, *Ketengus* and *Potamarius* also. The epioccipital invades the skull roof as an additional dermal skull bone in other ariid taxa (e.g., *Netuma proximus*, *Aspistor hardenbergi*, *Hemiarius sona*, *Bagre marinus*). *Cryptarius* shares with *Amissidens* the small mouth, restricted gill openings and partially united gonads, but it differs in having low buccopharyngeal pads and flaps (well developed in *Amissidens*), few gill rakers (28–37 in *Amissidens*), the epioccipital invading the skull roof, the wedge-shaped vomer and the excavated laminar bone (extensive laminar bone in *Amissidens*).

Distribution. Thailand, Cambodia/Vietnam (Rainboth 1996), western Indonesia and the western Malay Peninsula. Coastal waters, estuaries and rivers.

Taxa. Possibly two valid species: *Cryptarius truncatus* (Valenciennes, 1840a) (synonym: *Hemipimelodus cochlearis* Fowler, 1935) and *C. daugueti* (Chevey, 1932). I have not seen type material of *Hemipimelodus daugueti*.

Galeichthys Valenciennes, 1840

Galeichthys Valenciennes, 1840: 28 (type species *Galeichthys feliceps* Valenciennes, 1840, by subsequent designation by Bleeker 1862 and 1863).

Diagnosis. *Galeichthys* is the only ariid genus which does not possess all of the thirteen characters which together identify the Ariidae from all other siluroids (see above, Monophyly of the Ariidae). The epioccipital bone is only slightly produced posteriorly and does not contact the dorsal surface of the superficial laminar bone of the anterior complex vertebrae (character 3; in other ariids the produced epioccipital usually articulates with the laminar bone). The aortic tunnel formed by the laminar bone of the fused anterior vertebrae is abbreviated, or absent (*G. peruvianus*) (character 4; the bone spreads over the canal in other ariids, forming a tunnel). There is a supraneural between the supraoccipital and the nuchal plate which is exposed in the dorsal surface (character 5; in other ariids the supraoccipital articulates with the nuchal plate). The lapillus otolith is small (character 7; larger in other ariids), and the Mullerian ramus is attached to the ossified Baudelot's ligament of the supracleithrum, meaning that it lacks elasticity (Kulongowski 2001) (character 8; in other ariids, muscles connect the Mullerian ramus to the anterior vertebrae and the neurocranium). The subvertebral cone is low and has a deep median excavation. The five or six pores in the mandible are large, and rakers are present along the back of all gill arches.

Galeichthys possesses several derived features. The oblique laminae of the second and third neural spines are high and a lamina extends downwards also from the ventral surface of the supraoccipital; the posterior cleithral process is broad and fan-shaped; the temporal fossa is small; the almost smooth neurocranium is covered by thick skin and/or muscle layers; the supraoccipital is long and narrow and its sides are almost parallel; and the fin spines are moderately thin. Furthermore, there are no pads on the inner pelvic fin rays of mature females.

Galeichthys feliceps: Br 6. A. 17–19. P. I,10–12. Total gill rakers (first arch) 11–14. Vertebrae 6+11–12+5–6+34–35, total 51–53.

All species: Br 6. A 15–20. P. I,9–13. Total gill rakers (first arch) 10–15. Vertebrae 6+11–20+5–6+29–32, total 51–57.

Comparisons. In all other ariids the epioccipital is much extended and approximates the dorsal surface of the superficial laminar bone over the anterior fused vertebrae, the supraneural is not exposed in the dorsal surface, the lapillus otolith is larger and the Mullerian ramus is attached to the posterior wall of the neurocranium by the ESA. Although in most other ariids the laminar bone of the anterior vertebral region covers all of the centra (so forming the aortic tunnel), in some species of *Hemiarius* it is abbreviated also, exposing an aortic canal. Other genera lacking pads on the pelvic fin of mature females include *Cinetodus*, *Nedystoma*, *Osteogeneiosus*, *Cathorops* and *Sciades*.

Distribution. South-west to south-east Africa; western South America. Sea, estuaries and lower reaches of rivers.

Taxa. Four valid species: *Galeichthys ater* Castelnau, 1861; *G. feliceps* Valenciennes, 1840a (synonyms: ?*Pimelodes fossor* Lichtenstein, 1823; *Pimelodus peronii* Valenciennes, 1840; *Bagrus capensis* Smith, 1840; *Galeichthys ocellatus* Gilchrist and Thompson, 1916); *G. peruvianus* Lütken, 1874; and an undescribed species (Kulongowski 2001).

Hemiarius Bleeker, 1862

Hemiarius Bleeker, 1862: 7, 29 (type species *Cephalocassis stormii* Bleeker, 1858, by original designation).

Notarius Gill, 1863: 171 (type species *Arius grandicassis* Valenciennes, 1840a, by monotypy).

Diagnosis. *Hemiarius* is remarkable for its prominent ('shark'-like) snout and thick lips, strong jaws (lower upturned at symphysis) and wide mouth, strong and fixed, sharp teeth (those in upper jaw exposed when the mouth is shut), small eye, wide gill openings and low number (10–18) of stiff gill rakers. The chin barbel bases are well-staggered. In species other than *H. insidiator*, the fin spines are thick and rugose, flattened and chambered, and the sides of the swim bladder are scalloped externally.

The skull surface is smooth (often with a network of fine venules) to very granular (*H. sona*). The subvertebral cone is moderately to well-elevated, the mesethmoid is convex and broad (fluted and ridged in *H. grandicassis*), and the metapterygoid is enlarged and extends beyond the hind margin of the quadrate (in line with the hind margin of the quadrate in *H. stormii*). The laminar bone over the anterior fused vertebrae is not extensive and is deeply excavated medially, exposing the bases of the fourth to sixth transverse processes (not so in *H. sona*). The mandibulary pores are large. The large temporal fossa remains open at all life stages and the broadly rounded or elongate posterior dorsomedian fontanelle either remains large (*H. stormii*) or reduces in size with growth. In *H. grandicassis* the supraoccipital process is expanded and ovate (triangular or oblong in other taxa). The epioccipital invades the skull roof in *H. sona*, the extrascapular remaining as a distinct bone. The frontal bones are either broader posteriorly with large lateral ethmoid-frontal space (*H. stormii, H. grandicassis*) or broad anteriorly with a small lateral ethmoid-frontal space. The pectoral girdle is shallowly curved.

The jaw teeth are arranged in 2–5 well-spaced series and the four palatal tooth patches (two vomerine, two autogenous) are either small and narrow or large (*H. grandicassis, H. sona*). Rakers are absent from the back of all gill arches (except in *H. sona*) and the barbels are short and strap-like (mandibulary barbel long in *H. insidiator*). The supraoccipital process is broadly triangular, or elongate (*H. insidiator*) or ovate and expanding with age (*H. grandicassis*). The adipose fin is long-based (short-based in *H. insidiator*). The swim bladder is triangular with scalloped sides (more rounded and smooth-sided in very small fish) or flat and board-like with smooth sides (*H. insidiator*). Pads are present on the pelvic fins of mature females (unknown for *H. insidiator*).

Hemiarius stormii: Br 6. A. 17–20. P. I,11–12. Total gill rakers (first arch) 10–11. Vertebrae 6+15+5+28–29, total 49–50.

All species: Br 6–7. A 15–21. P. I,10–12. Total gill rakers (first arch) 10–18. Vertebrae 5–7+11–15+3–6+23–33, total 46–60.

Comparisons. The Mullerian ramus in *H. dioctes* is long (as in *Amissidens hainesi, Cinetodus* and *Nedystoma dayi*) or abbreviated and angular (*H. insidiator*). Albeit flattened fin spines are characteristic of *Hemiarius*, that character state appears in *Batrachocephalus*, *Aspistor hardenbergi* and *Hexanematichthys*. *Hemiarius dioctes* and *H. insidiator* share possession of seven branchiostegal rays with *Nemapteryx augustus*, cf. *Arius macrorhynchus* and *Arius platystomus* (Tilak 1965). In *H. insidiator* the uncinate process of the third epibranchial overlaps the proximal part of the fourth epibranchial and the eye is subcutaneous (both states also in *Nedystoma novaeguineae* and perhaps other ariids), the underside of the mesethmoid becomes concave with ontogeny (also in *Cochlefelis spatula*) and the parapophysis emanating from the fifth vertebra is expanded and angled forward slightly (also in some *Cathorops, Genidens* and *Potamarius*). *Hemiarius insidiator* is a most peculiar ariid: the body is much depressed and the ribs are long and angular, impressed in the abdominal body wall; the swim bladder is long and oval, board-like, and internally divided by numerous septae (its length surely associates with the long abdominal cavity and high number (27–28) of precaudal vertebrae); the nasal bone is broad and peculiarly shaped; and the fin spines are very thin, somewhat flexible, and scarcely serrate. There are no collagen rods in the barbels of *H. insidiator* (refer Character 75).

Distribution. South-east Asia (Pakistan to Sumatra and Borneo: three species); southern New Guinea (two species); north-eastern South America (one species). Inshore marine waters and estuaries, to fresh water.

Taxa. Six valid species: *Hemiarius dioctes* (Kailola, 2000); *H. grandicassis* (Valenciennes, 1840a); *H. insidiator* (Kailola, 2000); *H. sona* (Hamilton, 1822) (probable synonym: *Hexanematichthys leptocassis* Bleeker, 1861); *H. stormii* (Bleeker, 1858); and *H. verrucosus* (Ng, 2003).

Literature synonyms of *Arius sona* are *Bagrus trachipomus* Valenciennes, 1840 and *Bagrus gagorides* Valenciennes, 1840. I have not examined type material. A literature synonym of *H. grandicassis* is *Arius stricticassis* Valenciennes, 1840a; however some authors (e.g., Jordan and Evermann 1896–1900; van der Stigchel 1946) consider that *A. stricticassis* is a valid species. I had insufficient material to decide this matter.

Comments. The synonymy of *H. leptocassis* (Bleeker) is advised by Heok Hee Ng (pers. comm.) based on his examination of a 127 mm SL Bleeker specimen (MCZ 159231) from Penang.

Hexanematichthys Bleeker, 1858

Hexanematichthys Bleeker, 1858: 24, 61, 126, 416 (also Bleeker, 1858a: 2) (type species *Bagrus sondaicus* Valenciennes, 1840, by monotypy).

Diagnosis. *Hexanematichthys* is recognised by the combination of a broad, depressed head and extensive, granular or rugose head shield, a dark (dusky brown or darkly-spotted) peritoneum, the nuchal plate ('predorsal plate') increasing in size and becoming square or 'butterfly'-shaped with age, and a long-based adipose fin.

The posterior dorsomedian fontanelle is small and extending backwards just a short distance past the eye, or absent; the supraoccipital process is broad and short; the temporal fossa is absent or very small; the frontal bone is extensive anteriorly such that the lateral ethmoid-frontal space is almost obliterated, and there are many (13–18) thoracic vertebrae.

The jaw and palate teeth are sharp and conical, forming either six (*H. mastersi*) or four (*H. sagor*) patches across the front of the palate. The barbels are strap-like, rakers are absent from the back of the first two gill arches (sometimes a few are present on the upper second arch in *H. mastersi*) and the gill openings are wide. On the snout there is always a short crescent-shaped groove between the nostrils. The fin spines are strong, compressed and coarsely striate, and are tipped with short filaments. Mature females have pads on the inner rays of the pelvic fins.

Hexanematichthys sagor: Br 6. A.16–20. P. I,9–11. Total gill rakers (first arch) 12–18. Vertebrae 6–7+13–14+5+28–29, total 53–55.

All species: Br 6. A. 16–20. P. I,9–11. Total gill rakers (first arch) 12–18. Vertebrae 6–7+13–18+5+28–32, total 53–61.

Comparisons. Members of *Sciades* and some *Aspistor* also have a predorsal plate expanding with age, and they and members of other genera (e.g., *Plicofollis* n. gen. *Arius*) have a very granular neurocranium. Some *Netuma* have three patches of teeth on each side of the palate (as has *H. mastersi*) but their arrangement differs. Only species of *Sciades* (and *Hemiarius insidiator*) have higher numbers of thoracic vertebrae than has *Hexanematichthys*. The broad spread of the frontal in *H. sagor* led Tilak (1965) to believe that it has only one lateral ethmoid-frontal articulation. I erred (Kailola 1999) when I stated that *Bagrus doroides* Valenciennes, 1840 – sometimes placed as a synonym of *H. sagor* – cannot be an ariid because it is recorded as having ossified plates along the first portion of the lateral line, as *Cinetodus froggatti* has such plates and Bhimachar (1933: 255) stated that in '*A. sagore* [sic] there are a few small bony ossicles posterior to the post-temporal enclosing portion of the lateral line canal.'

Distribution. India (east coast) to Java and Borneo (*H. sagor*); southern New Guinea and northern Australia (*H. mastersi*). Inshore coastal waters and estuaries.

Taxa. Two valid species: *Hexanematichthys mastersi* (Ogilby, 1898) (synonyms: *Tachysurus (Pararius) godfreyi* Whitley, 1941; *Arius sagoroides* Hardenberg, 1941); *H. sagor* (Hamilton, 1822) (synonyms: *Bagrus doroides* Valenciennes, 1840; ?*Bagrus javensis* Valenciennes, 1840; *Bagrus sondaicus* Valenciennes, 1840; *Hexanematichthys sundaicus* Bleeker, 1858 and *Arius leptaspis* Herre, 1935 (non Bleeker)).

Comments. In this genus are two good examples of 'replacement' species: one on the Sunda Shelf (*H sagor*) and the other on the Sahul Shelf (*H. mastersi*).

Ketengus Bleeker, 1847

Ketengus Bleeker, 1847: 9, 167 (type species *Ketengus* typus Bleeker, 1847, by original designation).

Diagnosis. The wide mouth of *Ketengus* extends well past the eye and the six barbels (three pairs) are short, equal to or shorter than the eye diameter. *Ketengus* has a single lateral ethmoid-frontal connection.

The jaws are strongly ossified and the cranial bones are smooth to striate. The mesethmoid is broad and truncate anteriorly and the nasal bone is an irregularly curved tube. The temporal fossa and the posterior dorsomedian fontanelle are usually absent. The hind margin of the large metapterygoid extends well beyond the hind margin of the quadrate. Although the first two (outer) branchiostegal rays in all ariids are broader than the remaining rays, in *Ketengus* they are exceptionally broad. The shape of the urohyal bone is broad and truncate anteriorly. The pelvic girdle is strong and the cleithrum high; the secondary hypurapophysis of the caudal skeleton is (occasionally) flattened and 'tear-drop' shaped; and the pelvic fin rays bear low ridges.

The snout is abrupt; the upper jaw overhangs the lower jaw and the broad lip has a crenulate inner margin. Each jaw possesses a single series of incisor-like, sometimes spatulate, teeth with short cusps. There are no teeth on the palate. There are rakers along the back of all gill arches, the gill openings are much restricted, the posterior cleithral process is short, the swim-bladder shape is almost triangular and the fin spines (especially the pectoral) are thick and strongly serrated. The lateral line is sometimes bifurcate at the tail base, sometimes single. The condition of the inner pelvic fin rays in females is unknown.

Br 5 or 6. A.19–21. P. I,7–8. Total gill rakers (first arch) 15. Vertebrae 6+9+4–5+27–29, total 47–49.

Comparisons. *Batrachocephalus* and *Osteogeneiosus* are other ariids having strongly ossified and heavy jaws. Other ariids with broad branchiostegals one and two are *Cathorops, Plicofollis* n. gen. and *Batrachocephalus*, and ridged pelvic fin rays also occur in *Cephalocassis borneensis, Cryptarius truncatus* and *Aspistor platypogon*. Members of *Plicofollis* n. gen. possess a 'tear-drop' shaped secondary hypurapophysis. In *Cephalocassis* and some *Cathorops* taxa the urohyal is broad and truncate also. *Batrachocephalus, Hemiarius dioctes* and *H. stormii* have triangular swim bladders.

Distribution. South-east Asia (Sunda Shelf) from the Andaman Islands to Malaya, Thailand, Java and Borneo. Inshore coastal waters and tidal reaches of rivers.

Taxa. One valid species: *Ketengus typus* Bleeker, 1847. Synonym from literature: *Pimelodus pectinidens* Cantor, 1849.

Nedystoma Ogilby, 1898

Nedystoma Ogilby, 1898: 32 (type species *Hemipimelodus dayi* Ramsay and Ogilby, 1886, by original designation).

Doiichthys Weber, 1913: 532 (type species *Doiichthys novaeguineae* Weber, 1913, by monotypy).

Diagnosis. This taxon is distinguished by possessing a reduced gonad (in which the gonad forms a single, ovate unit having an internal, incomplete septum) and mature females lacking pads or any form of thickening on the inner pelvic fin rays. *Nedystoma* species have a narrow band of very small teeth in each jaw, 29–51 rakers on the first gill arch, rakers present along the back of all gill arches, well-elevated subvertebral cone, and a large and rounded posterior dorsomedian fontanelle in a smooth neurocranium.

In *Nedystoma* the supraoccipital is slender and rectangular. The subvertebral cone is strong, the temporal fossa is small and reduced, and the frontal has narrow anterior arms and is broad posteriorly. The laminar bone over the anterior vertebrae is very extensive and may bear depressions; the posteromedian excavation of the laminar bone is shallow. The Mullerian ramus is long and the fourth neural spine is high and abuts the well-developed posteromedian flange of the epioccipital, especially in *N. dayi*. The premaxillary is thin, the pores in the mandible are moderately large (*N. dayi*) or very large (*N. novaeguineae*). The mesethmoid is convex (*N. novaeguineae*) or notched (*N. dayi*) and the nasal and lachrimal bones are irregularly-shaped (*N. novaeguineae*) or rod-like and curved (*N. dayi*). *Nedystoma novaeguineae* has seven infraorbital bones and *N. dayi* has four. The posterior cleithral process is short and acute. Branchiostegals are slender and elongate, the pectoral girdle is strong and compact, the lateral arms of the urohyal are slender and tend to bifurcate distally, and the elliptical uncinate process of the third epibranchial overlaps the proximal portion of the fourth epibranchial. There is a long facet between the palatine bone and the lateral ethmoid.

The slender jaw teeth comprise 1–4 narrow series in upper jaw, 1–3 in lower jaw; and there are no (*N. dayi*) or four small (*N. novaeguineae*) patches of teeth on the palate. In *N. novaeguineae* the gill openings are very wide, there are no buccopharyngeal flaps, the eye is covered with skin, the chin barbel bases are well-staggered, the parapophyses from the fifth vertebra are directed at right angles to the vertebra centrum, and the fin spines are strong with large serrae. In *N. dayi* the gill openings are much restricted, there are large buccopharyngeal flaps, the eye is almost free of skin, the chin barbel bases are close together, the parapophyses from the fifth vertebra are directed posterolaterally and the fin spines are thin.

Nedystoma dayi: Br 6. A. 19–24. P. I,10–11. Total gill rakers (first arch) 29–43. Vertebrae 6+7–9+4–6+29–30, total 47–49.

All species: Br 6. A. 19–33. P. I,9–11. Total gill rakers (first arch) 29–51. Vertebrae: 6+7–9+2–6+29–35, total 47–52.

Comparisons. The long facet between the palatine bone and the lateral ethmoid of *Nedystoma* occurs also in *Brustiarius* and *Plicofollis* n. gen.. Only *Brustiarius nox* (56–67), *Amissidens hainesi* (28–37) and *Cathorops hypophthalmus* (37–41) have more gill rakers on the first arch. *Nedystoma dayi* has affinities with *Amissidens hainesi* and *Cephalocassis* species in the restricted gill openings and large buccopharyngeal pads, and *N. novaeguineae* shares with *Nemapteryx armiger* characters such as widely staggered chin barbels, wide gill openings, and palate dentition. The subcutaneous eye (of *N. novaeguineae*) is a state that has arisen independently in some other ariids (e.g., *Cathorops hypophthalmus, Cephalocassis* species, *Hemiarius insidiator*).

Distribution. Sahul Shelf (southern New Guinea). Fresh water to brackish/estuarine.

Taxa. Two species: *Nedystoma dayi* (Ramsay and Ogilby, 1886); *N. novaeguineae* (Weber, 1913).

Nemapteryx Ogilby, 1908

Nemapteryx Ogilby, 1908: 10 (type species *Arius stirlingi* Ogilby, 1898 by original designation).

Diagnosis. This genus is characterised by strong and sharp, usually non-depressible teeth on the jaws and palate, and strong jaws, the lower jaw symphysis inclined upward. The posterior dorsomedian fontanelle is open and deep at all stadia (except for one species), the four ridges along the head shield are always prominent, the chin barbels are strongly staggered and the dorsal spine bears a filament at all stadia.

The mesethmoid is shallowly notched or truncate, the frontal–lateral ethmoid space is either large or moderate, and the temporal fossa is large. The metapterygoid is forward in position. The subvertebral cone is high (*N. armiger*) or low (*N. augustus*). The mandibulary pores are large. The posterior cleithral process is short (*N. armiger*) or moderately long.

The mouth is strongly curved and the gape is wide. On the palate, there are a pair of small vomerine patches of teeth (*N. armiger, N. nenga, N. augustus*) (and) large, triangular, ovate or 'pear'-shaped autogenous plates laterally. The eye is small (*N. armiger, N. augustus*) to large and may be dominated by the lateral ethmoid; the posterior dorsomedian fontanelle is deep and 'tear-drop' shaped (reducing in size with age in some species); the head shield varies from rough and striated to very granular, the granules arranged in clusters. The triangular supraoccipital process is strongly keeled. The gill openings are wide; rakers present on or absent from (*N. armiger, N. bleekeri*) the back of the first two gill arches; the barbels are thick and long, strap-like, the maxillary barbels are long, 26–45% SL (not in *N. augustus*, where the barbels are thin and only 10–12% of SL). The dorsal spine is strong and thick (especially basally), rugose, pitted and chambered (*N. nenga, N. macronotacanthus*) (not in *N. armiger*, where it is thin), its edges granulated or serrated. All fin spines are long (65–95% HL). The adipose fin is usually short-based and may bear a large dark patch, and the lateral line is bifurcate or turned dorsad (*N. armiger, N. bleekeri, N. augustus*) at the tail base.

Nemapteryx armiger: Br 6. A. 22–25. P. I,9–11. Total gill rakers (first arch) 16–22. Vertebrae 15–17+5+30–31, total 52.

All species: Br 6–7. A. 17–25. P. I,9–11. Total gill rakers (first arch) 12–22. Vertebrae 15–19+5–6+30–33, total 52–58.

Comparisons. Ogilby (1908) characterised *Nemapteryx* by the long filament on the dorsal fin (retained in adults), villiform teeth, four tooth patches across the front of the palate, long barbels and small eye. *Nemapteryx* is closest to *Hemiarius* species with which it shares the strong, fixed teeth, wide gill openings, large mandibulary pores and temporal fossa, and staggered chin barbels. *Nemapteryx armiger* differs from most *Hemiarius* chiefly in having a high subvertebral cone and short posterior cleithral process, and other *Nemapteryx* species differ from *Hemiarius* in their truncate rather than convex mesethmoid, less extensive laminar bone, and smooth-edged swim bladder. *Nedystoma novaeguineae* can be compared with *Nemapteryx* by its wide gill openings and well-spaced chin barbel bases.

In earlier work in Indonesia (Kailola 1981) I was impressed that *Arius caelatus* (= *Nemapteryx nenga*) seemed to be a Sunda Shelf 'replacement species' for the Sahul Shelf *N. armiger*, and the diet of both taxa comprised mainly prawns (Penaeidae). Indeed, Fowler (1928: 62) recorded that *N. armiger* 'is possibly related to, if not synonymous with, *Tachysurus caelatus* (Val.)'.

Distribution. India to Java (three species); southern New Guinea and northern Australia (two species); ?Malaya (one species). Inshore coastal and estuarine waters.

Taxa. Probably six valid species: *Nemapteryx armiger* (de Vis, 1884) (synonym: *Arius stirlingi* Ogilby, 1898); *N. augustus* (Roberts, 1978); ?*N. bleekeri* (Popta, 1900) (said by Eschmeyer (1998) to be from the Malay Archipelago); *N. macronotacanthus* (Bleeker, 1846) (probable synonym: *Arius parvipinnis* Day, 1877); *N. nenga* (Hamilton, 1822) (synonym: *Arius caelatus* Valenciennes 1840a). An unnamed species is represented by material in several collections from Thailand, Pakistan, Singapore, Malaysia and Sri Lanka.

Literature synonyms of *Arius caelatus* are *Arius aequibarbis* Valenciennes, 1840a; *A. granosus* Valenciennes, 1840a; *A. caelatoides* Bleeker, 1846; *A. chondropterygius* Bleeker, 1846; *A. clypeaster* Bleeker, 1846; *A. clypeastroides* Bleeker, 1846; *A. microgastropterygius* Bleeker, 1846; and *A. melanopterygius* Bleeker, 1849. A literature synonym of *Arius macronotacanthus* is *A. arius* Cantor, 1849 (non Hamilton) and a literature synonym of *Arius nenga* is *Bagrus arioides* Valenciennes, 1840. I have not examined type material of these taxa.

Comment. Interestingly, Day (1877) labelled his figure of *A. parvipinnis* as *A. macronotacanthus*, endorsing his remark (p. 461) that the two species are 'evidently closely allied'. I am uncertain of the status of *N. bleekeri* (Popta) which is based on only two specimens, 114 mm SL and 124 mm SL.

Netuma Bleeker, 1858

Catastoma Valenciennes, 1840a: 60 (based on *Catastoma nasutum* Kuhl and van Hasselt, MS).

Sarcogenys Bleeker, 1858: 96 (based on *Sarcogenys rostratus* Kuhl and van Hasselt, MS).

Netuma Bleeker, 1858: 23, 61, 62, 67, 93 (type species, *Bagrus netuma* Valenciennes, 1840, by monotypy).

Pararius Whitley, 1940: 409 (type species, *Arius proximus* Ogilby, 1898, by original designation).

Diagnosis. Species of *Netuma* are identified easily by their tapered, falcate caudal fin lobes, the 'V'-shaped posterior apex of the dorsomedian head groove formed by the frontals, their small-based adipose fin placed over the posterior of the anal fin, their streamlined body shape and somewhat prominent snout (especially in adult *N. thalassinus*), their large, triangular autogenous tooth patches placed beside the much smaller vomerine tooth patches (four patches in *N. thalassinus* and *N. bilineatus*, two in *N. proximus*) and scalloped swim bladder.

The head shield is rugose or slightly granular and the frontal bones are tapered posteriorly, the space between the lateral ethmoid and frontal bones reduced. The mesethmoid is notched with narrow cornuae, and smooth (*N. bilineatus, N. proximus*) or prominent and convex, the bone fluted and ridged (*N. thalassinus*). The nasal is curved and aligned with the curve of the mesethmoid neck. The frontal is much expanded anteriorly (similar to *Bagre* species) and in *N. bilineatus* the lateral ethmoid is expanded and closes off the space between it and the frontal. The temporal fossa is much reduced, or absent in *N. bilineatus*. The epioccipital invades the skull roof in *N. proximus* (not in *N. thalassinus*, *N. bilineatus*) while the extrascapular remains as a separate bone. There are 5–6 branchiostegals. In *N. thalassinus* the fin spines are half-chambered and the centra of the anterior caudal vertebrae are twice wider than the remaining centra. The caudal skeleton of *N. thalassinus* and *N. proximus* bears the apomorphy of the parahypural being sutured with hypurals 1 + 2.

Netuma lack gill rakers along the back of the first two gill arches but occasionally there are several rakers on the upper limb. The gill openings in *N. proximus* are less wide than are those of the other taxa; the lateral line bifurcates at the tail base (infrequently so in *N. proximus*). The swim bladder is heart-shaped and its sides are scalloped, and mature females develop pads on their inner pelvic fin rays.

Netuma thalassinus: Br 5. A. 14–17. P I,10–12. Total gill rakers (first arch) 12–15. Vertebrae 6+13–14+6+19–22, total 46–48.

All species: Br 5–6. A.14–21. P. I,10–12. Total gill rakers (first arch) 10–16. Vertebrae 6+12–15+6–9+19–28, total 46–58.

Comparisons. A fluted, convex mesethmoid also occurs in *Hemiarius grandicassis*, and cf. *Arius macrorhynchus*. In *Plicofollis* n. gen. *nella* and *Cinetodus crassilabris* also the parhypural is sutured with hypurals 1 + 2. A scalloped swim bladder is common to *Hemiarius* and *Plicofollis* n. gen. *Osteogeneiosus* and *Cryptarius*. In some earlier analyses (Kailola 1990) *N. proximus* aligned with *Aspistor hardenbergi* because of the epioccipital invading the skull roof and the absence of posterior gill rakers. A small adipose fin also occurs in *Brustiarius* species, *Bagre*, cf. *Arius macrorhynchus* and *Amissidens hainesi*.

Distribution. East Africa to Asia (not *N. proximus*) to New Guinea and Australia. Marine to nearshore, also entering estuaries and embayments.

Taxa. Three valid species: *Netuma bilineatus* (Valenciennes, 1840) (synonyms: *Bagrus rhodonotus* Bleeker, 1846; *Arius andamanensis* Day, 1871 (in part); *Arius serratus* Day, 1877 (in part); *Netuma osakae* Jordan and Kanazawe in Jordan and Hubbs, 1925; *Arius dayi* Dmitrenko, 1974); *N. proximus* (Ogilby, 1898) (synonyms: *Arius graeffei* Paradice and Whitley, 1927 (non Kner and Steindachner); *Arius arafurensis* Hardenberg, 1948); *N. thalassinus* (Rüppell, 1837) (synonyms: *Bagrus laevigatus* Valenciennes, 1840; *Bagrus netuma* Valenciennes, 1840; *Arius nasutus* Valenciennes, 1840a; *Bagrus carchariorhynchos* Bleeker, 1846; *Sarcogenys rostratus* Bleeker, 1858; *Arius andamanensis* Day, 1871 (in part); *Arius serratus* Day, 1877 (in part); *Ariodes aeneus* Sauvage, 1883; *Netuma thalassina jacksonensis* Whitley, 1941). Based on its head shape, falcate caudal fin lobes, and small-based and posteriorly situated adipose fin (Whitehead 1969) *Galeichthys stanneus* Richardson, 1846, is a probable synonym of either *N. bilineatus* or *N. thalassinus*.

Comments. Consult Kailola (1986) for further information on *N. bilineatus* and *N. thalassinus*.

Osteogeneiosus Bleeker, 1846

Osteogeneiosus Bleeker, 1846: 173 (type species *Arius militaris* Linnaeus, 1758, by subsequent designation of Bleeker, 1862).

Diagnosis. *Osteogeneiosus* is characterised by its possession of a pair of maxillary barbels (only), those barbels being long and stiff, supported by an extensive and strongly ossified maxilla.

The subvertebral cone is moderately high, the posterior cleithral process is short, the mesethmoid has broad cornuae and an almost truncate anterior margin. The nasal bone is curved, the lachrimal peculiarly shaped. The hind margin of the metapterygoid extends well beyond the hind margin of the quadrate. The temporal fossa and the posterior dorsomedian fontanelle reduce in size with growth. The frontals are broader posteriorly with long and slender anterior arms;

the bone tissue in the lateral ethmoid is 'honeycombed' (vacuolated). The mandibulary pores are small.

The head is strongly depressed. The jaw teeth form a single band in each jaw and the blunt teeth on the palate form two large elliptical patches near the palate margins; there are no vomerine teeth. The skull is heavily ossified (especially posteriorly); the neurocranium rugose, granular or sculptured but covered with smooth skin; the supraoccipital is elongate. The gill openings are wide, there are long and slender rakers along the back of all gill arches, the inner rays of the pelvic fin in mature females are thickened and the lateral line bifurcates at the tail base. The sides of the heart-shaped swim bladder are scalloped externally.

Br 6. A. 19–22. P. I,9–10. Total gill rakers (first arch) 10–11. Vertebrae 6+11+6+28–30, total 51–53.

Comparisons. A 'honeycombed' lateral ethmoid is a feature of some species of *Plicofollis* n. gen. also. Other taxa possessing a scalloped swim bladder are *Cryptarius truncatus* and some taxa within *Plicofollis* n. gen. *Netuma* and *Hemiarius*.

Distribution. India to South-east Asia. Coastal waters, lower reaches of rivers and estuaries; freshwater?

Taxa. One valid species: *Osteogeneiosus militaris* (Linnaeus, 1758). Literature synonyms are: *Osteogeneiosus blochii* Bleeker, 1846; *O. gracilis* Bleeker, 1846; *O. ingluvies* Bleeker, 1846; *O. longiceps* Bleeker, 1846; *O. macrocephalus* Bleeker, 1846; *O. valenciennesi* Bleeker, 1846; *O. cantoris* Bleeker, 1853; *O. sthenocephalus* Day, 1877. Types of these taxa were not examined.

Although Eschmeyer (1998: 1095) recorded *Silurus militaris* Linnaeus as the type of *Osteogeneiosus*; in the same work (p. 2050) he stated that the type is *Arius militaris* Valenciennes, 1840a.

Plicofollis new genus

Type species: *Arius argyropleuron* Valenciennes, 1840a: 104, by original designation.

Diagnosis. The new genus *Plicofollis* is characterised by the combination of having four autogenous tooth plates (two pairs) longitudinally arranged on the palate, an enlarged, rounded 'head' and short arms on the vomer, shortened and vertically extended distal caudal vertebral centra (in at least four taxa), and swim bladder with scalloped or creased sides.

The neurocranium is granular and striate to rugose, and in *P. nella* the supraoccipital process expands with age, becoming large and ovate. The anterior margin of the mesethmoid is notched to convex; the lachrimal bone is flattened and has extremely produced angles; the epioccipital invades the skull roof in some species (e.g., *P. nella, P. dussumieri*) but not in others (e.g., *P. argyropleuron*) while the extrascapular remains as a distinct bone. The temporal fossa is open throughout growth except in *P. dussumieri*, in which it is closed over in large fish. The metapterygoid is enlarged and extends well beyond the hind margin of the quadrate, and its suture with the hyomandibular is short to moderately wide. The elongate posterior dorsomedian fontanelle reduces in size with growth; the frontals are broad, the anterior space between its arms and the lateral ethmoid reducing with age as the frontal expands; and the laminar bone over the anterior vertebrae is extensive, concealing the bases of the fourth to sixth transverse processes and with only a shallow, median excavation. In some species (*P. dussumieri, P. nella, P. crossocheilos*) the lateral ethmoid 'wing' becomes extremely large: it is ovate or rectangular and consists of honeycomb-textured or papyraceous bone (as is the bone structure of the expanded supraoccipital process in *P. nella*).

The mouth is moderately small and the jaw tooth bands are short. The jaw teeth are slender, there are no teeth on the vomer, and the conical or molariform palatal teeth are arranged in two patches each side (one behind the other): many or all of the teeth in the front patch are frequently missing, and teeth in the second patch are sometimes lost also. The head is moderately long and the dorsomedian fontanelle is long – from the snout to the base of the supraoccipital process. Rakers are absent from the back of the first and sometimes second gill arches. The gill openings are reduced, the membranes meeting at an obtuse angle across the isthmus, and the barbels are moderately thick and fleshy, those on the mandible with their bases close together and almost aligned. The lateral line bifurcates at the tail base, the adipose fin lies over the middle of the anal fin, and the fin spines are robust, chambered in larger fish. The sides of the swim bladder are smooth externally and creased or scalloped internally, or creased internally and externally (*P. argyropleuron*), and pads develop on the inner pelvic fin rays in mature females.

Plicofollis argyropleuron: Br 6. A. 14–21. P I,10–12. Total gill rakers (first arch) 10–16. Vertebrae 6–7+9–12+6–7+32–33, total 48–51.

All species: Br 6. A. 14–21. P. I,10–13. Total gill rakers (first arch) 10–17. Vertebrae 6–7+9–15+4–7+22–27, total 45–51.

Etymology. From *plico* (Latin) meaning fold, and *follis* (Latin) meaning bellows or windbag (Brown 1956), in reference to the creased or scalloped swim bladder characteristic of this group.

Comparisons. As in most ariid genera, some derived features of *Plicofollis* are shared with other taxa. For example, the facet between the palatine bone and the lateral ethmoid is long (also in *Nedystoma dayi* and *Brustiarius*), the first branchiostegal is very broad (also in *Cathorops, Ketengus, Batrachocephalus*), the form of the secondary hypurapophyses of the caudal skeleton in *P. argyropleuron* is similar to that of *Ketengus*, *Osteogeneiosus* also develops an expanded lateral ethmoid comprising 'honeycomb'-textured bone, chambered fin spines occur in *P. dussumieri* and *P. nella* (also in some *Hemiarius*, *Cephalocassis melanochir*, and several other ariid taxa), and large individuals of *Plicofollis* (e.g., *P. nella*) occasionally develop extra tooth patches (as occurs also in *Arius dispar*, some *Aspistor* and some *Sciades*). The first two branchiostegals are noticeably broad, as in *Ketengus*, *Cathorops* and *Batrachocephalus*. Because I have examined very little skeletal material of some species (e.g., *P. layardi*, *P. crossocheilos*, *P. dussumieri*) I am unable to comment on the extent of certain characters in the genus; for example, in the caudal skeleton: *P. argyropleuron* has a 'teardrop'-shaped secondary hypurapophyses but this state is not present in *P. nella* and *P. polystaphylodon*; the distal caudal vertebrae do not appear to be significantly narrower than the proximal vertebrae in *P. crossocheilos* but they are in *P. magatensis* (*Bagre marinus* also has vertically elongate distal caudal vertebrae); and the parhypural is clearly sutured with hypurals 1 + 2 in *P. nella* but not in *P. argyropleuron* and *P. polystaphylodon*.

Distribution. East Africa to New Guinea and northern Australia. Marine to estuarine; freshwater (*P. magatensis*).

Taxa. At least seven valid species: *P. argyropleuron* (Valenciennes, 1840a) (synonyms: *Arius acutus* Bleeker, 1846; *Arius macrocephalus* Bleeker, 1846; *Arius hamiltonis* Bleeker, 1846; *Arius schlegeli* Bleeker, 1863; *Tachysurus broadbenti* Ogilby, 1908; *Hemipimelodus colcloughi* Ogilby, 1910); *P. crossocheilos* (Bleeker, 1846) (synonym: *Arius tonggol* Bleeker, 1846); *P. dussumieri* (Valenciennes, 1840a) (synonym: *Arius goniaspis* Bleeker, 1858); *P. layardi* (Günther, 1866) (synonyms: *Arius tenuispinis* Day, 1877; *Arius satparanus* Chaudhuri, 1916; *P. magatensis* (Herre, 1926); *P. nella* (Valenciennes, 1840a) (synonyms: *Arius leiotetocephalus* Bleeker, 1846; *Bagrus (Ariodes) meyenii* Müller and Troschel, 1849); and *P. polystaphylodon* (Bleeker, 1846).

Literature synonyms of *Plicofollis dussumieri* are *Arius kirkii* Günther, 1864 and possibly *Arius belangerii* Valenciennes, 1840a. I have not seen type material of these taxa.

Potamarius Hubbs and Miller, 1960

Potamarius Hubbs and Miller, 1960: 101 (type species *Conorhynchos nelsoni* Evermann and Goldsborough, 1902, by original designation).

Diagnosis. *Potamarius* is distinguished by the combination of an almost conical snout, thick lips and subinferior mouth, short barbels, eyes placed high on the head, tapered body, enlarged metapterygoid extending to above the hind margin of the quadrate, tiny mandibulary pores, parapophyses of the fifth and sixth vertebrae united and angled forward, and a toothless palate.

Potamarius has a well ossified skull. The subvertebral cone is moderately low and the flanges and ridges of the fourth neural spine and epioccipital are poorly developed. There is an apparent extrascapular, an enlarged metapterygoid where the hind border is well posterior and lies in line with the hind border of the quadrate, and an elongate hyomandibular. The lateral ethmoid is large, truncate and oblong, and posteriorly directed. The posterior dorsomedian fontanelle is elongate-rectangular and always open, the temporal fossa is large at all growth stages, and the mandibulary pores are tiny or concealed. The post-cleithral process is moderately long, and there is a strong, compact pectoral girdle and coracoid keel. The parapophyses of the fifth and sixth vertebrae are united and angled forward and form a peculiar shape. The basipterygium is enlarged and rounded.

The depressible jaw teeth lie in 10–12 series, and the palate is edentate. The chin barbel bases are generally close together and aligned, and there are large buccopharyngeal flaps and pads; the chin barbels in *P. nelsoni* have membranous inner margins. Rakers are present along the back of all gill arches; the gill membranes are free yet the openings are somewhat restricted. The pectoral axillary pore is large. The fin spines are thick and the pectoral spines bear strong dentae along their inner edge. The adipose fin lies above the middle of the anal fin, the peritoneum is pale, fleshy pads develop on the inner pelvic fin rays of mature females and the gonad is bilobate.

All species: Br – (not available). A.15–21. P. I, 9–10. Total gill rakers (first arch) 14–18. Vertebrae 7+10–11+4–5+30, total 52–54.

Comparisons. *Potamarius* is comparable with *Cinetodus* (shares 33 character states) and possibly also with *Cathorops*. *Cinetodus* however, is distinct in the absence in mature females of pads on the pelvic fins, the presence of a strongly-elevated subvertebral cone, high ridges and flange to the epioccipital, large mandibulary pores and restricted gill openings. With *Cathorops*, *Potamarius* shares the character state of the parapophyses of the fifth and sixth vertebrae being united and angled forward (in most other ariids the parapophyses are directed posterolaterally; or at right angles). *Cinetodus* and *Aspistor hardenbergi* also have an enlarged axillary pore. Species of *Plicofollis* and *Hemiarius grandicassis* share with *Potamarius* the character of an enlarged, oblong lateral ethmoid.

Distribution. Central America. Fresh water.

Taxa. Three valid species: *Potamarius izabelensis* Hubbs and Miller, 1960; *P. nelsoni* (Evermann and

Goldsborough, 1902); and (following Marceniuk and Ferraris Jr 2003) *P. grandoculis* (Steindachner, 1877a).

Sciades Müller and Troschel, 1849

Sciades Müller and Troschel, 1849: 6 (type species *Bagrus (Sciades) emphysetus* Müller and Troschel, 1849, by subsequent designation by Bleeker 1862).

Selenaspis Bleeker, 1858: 62, 66 (type species *Silurus herzbergii* Bloch, 1794, by subsequent designation by Jordan and Evermann 1896).

Sciadeichthys Bleeker, 1858: 62, 66 (type species *Bagrus (Sciades) emphysetus* Müller and Troschel, 1849, by monotypy).

Leptarius Gill, 1863: 170 (type species *Leptarius dowii* Gill, 1863, by monotypy).

Sciadeops Fowler, 1944: 211 (type species *Sciades troschelii* Gill, 1863, by original designation).

Diagnosis. *Sciades* is characterised by the combination of a broad, granular head, an obtuse snout, a short and broad supraoccipital, the predorsal bone ('nuchal plate') increasing in size with growth and becoming large, 11–20 thoracic vertebrae and a two-chambered swim bladder.

The mesethmoid is convex to shallowly notched anteriorly and the nasal bones are curved. The frontals are very extensive anteriorly; the lateral ethmoid-frontal space is obscured or greatly reduced by the frontal and the underturned lateral ethmoid. The posterior dorsomedian fontanelle is short or absent. The vomer is 'T'-shaped and has a broad shaft. The subvertebral cone is low or moderately produced (*S. troschelii*). The epioccipital nudges but does not invade the skull roof and the extrascapular remains distinct, the temporal fossa is open or closed over; the mandibulary pores are moderately large (*S. troschelii*), tiny (*S. proops*) or closed. The laminar bone over the anterior fused vertebrae may be reduced posteriorly and in most species bears a deep pocket on each side of the central ridge. The flange of the Mullerian ramus is thin, the epioccipital flange extensive and the expansive supraoccipital and predorsal bone are supported underneath by a ridge and strut from the basioccipital and forward extensions of the fourth neural spine. The parapophyses from the fifth vertebra are turned outward in *S. proops* and *S. troschelii* (at least).

The snout is obtuse or prominent, and in some taxa it bears a transverse fold of skin between the nostrils. The skull surface is smooth to slightly granular anteriorly, strongly rugose and sharply granular posteriorly; the supraoccipital is triangular to almost square, short and broad, and the predorsal bone increases in size with growth, becoming either butterfly-shaped, rhombic ('shield'-shaped) or crescentic. The bone of the predorsal plate is 'honeycombed' (vacuolated). Teeth on the jaws and palate are villiform or finely conical. The vomerine tooth patches coalesce to form one patch with age; the palatal patches usually are much larger and elongate with irregular inner margins; and sometimes in larger fish (?females), oval patches of sharp teeth are present behind the palatal patches (parasphenoid and/or orbitosphenoid teeth). The barbels are strap-like, their bases strongly staggered on the chin; the gill openings are moderately wide; there are no rakers on the back of the first two gill arches and the buccopharyngeal pads are moderately developed. The broad posterior cleithral process bears radiating lines of granules; the axillary pore is small; the dorsal and pectoral fin spines are robust and coarsely granular, strongly serrated behind and laterally; the adipose fin is moderately large, and the lateral line turns upward at the tail base. The swim bladder is in two chambers (based on *S. emphysetus*): a heart-shaped anterior chamber connected to an elongate posterior chamber by a ductus pneumaticus. There are no pads on the pelvic fins of mature female *S. emphysetus* but the condition in other taxa is unknown.

Sciades emphysetus: Br 6. A. 18–21. P. I,12. Total gill rakers (first arch) 15–17. Vertebrae 7–8+16+4+29–30, total 56–57.

All species: Br 6. A 16–21. P. I,10–12. Total gill rakers (first arch) 16–24. Vertebrae 7–8+11–20+2–6+27–36, total 53–67.

Comparisons. *Sciades* is most similar to *Aspistor* and *Hexanematichthys*, as the genera share an expanded predorsal bone, broad granular head, strap-like barbels and high number of vertebrae. However, the distinguishing features of *Aspistor* and *Hexanematichthys* include the single swim bladder, the fewer (5–18) thoracic vertebrae and more haemal vertebrae (5–8, cf. 2–6 in *Sciades*), and the fewer gill rakers (11–18, cf. 16–24 in *Sciades*). The frontal-lateral ethmoid space becomes obscured also in *Hexanematichthys*. The forward-directed parapophyses of the fifth vertebra (in some *Sciades*) are found also in *Cathorops*; honeycomb-textured or 'porous' bones (predorsal plate in *Sciades*) also occur in some species of *Plicofollis, Osteogeneiosus* and *Bagre* (for example); and *Cinetodus, Nedystoma dayi* and *Guiritinga barbus* (at least) have 'pocketed' laminar shelves.

Distribution. North-eastern and north-western South America. Inshore marine.

Taxa. At least eight valid species: *Sciades couma* (Valenciennes, 1840); *S. emphysetus* (Müller and Troschel, 1849); *S. herzbergii* (Bloch, 1794); *S. hymenorrhinos* (Bleeker, 1862a) (synonyms (from Castro-Aguirre *et al.* 1999): *Arius alatus* Steindachner, 1877; *Leptarius dowii* Gill, 1863); *S. parkeri* (Traill, 1832); *S. passany* (Valenciennes, 1840); *S. proops* (Valenciennes, 1840); *S. troschelii* Gill, 1863. The apparently undescribed taxon '*usumacinctae* MS of Bailey' (MCZ museum labels) also belongs in *Sciades*.

A literature synonym of *Sciades couma* Valenciennes is *Sciaedeichthys (Selenaspis) walcrechti* Boeseman, 1954; literature synonyms of *S. herzbergii* Bloch include *Pimelodus argenteus* Lacépède, 1803, *Bagrus mesops* Valenciennes, 1840a and *Bagrus coelestinus* Müller and Troschel, 1849; of *S. parkeri* Traill are *Bagrus albicans* Valenciennes, 1840 and *Arius bonneti* Puyo, 1936; and of *S. troschelii* are *Bagrus temminckianus* Valenciennes, 1840 and *Arius brandtii* Steindachner, 1877. I have not seen type material of these taxa.

Comments. According to Fink and Fink (1996), a swim bladder with anterior and posterior chambers is characteristic of the Ostariophysi, and the general siluriform condition appears to be absence of the constriction separating the anterior and posterior chambers. In *S. emphysetus* (at least) the constriction is clear, the swim bladder comprising two, possibly three chambers, interconnected by short ducts. Howes (1985) reported additional swim bladder chambers on malapterurid catfishes and some pangasid catfishes.

Invalid genera

Paradiplomystes Bleeker, 1863

Paradiplomystes Bleeker, 1862:8 (type species *Pimelodus coruscans* Lichtenstein, 1819. Type by original designation; also by monotypy).

Paradiplomystax Günther, 1864, is an unjustified emendation (Eschmeyer 1998). The type species was described by Lichtenstein (1819) who had just one specimen, 75 mm long, said to be from Brazil. The name has remained in ariid systematic reports and is considered valid (Burgess 1989). However, according to W.R. Taylor (in litt. 1987) and H.J. Paepke (in litt. 1988) the specimen belongs in the Pimelodidae and is identical with *Hemisorubim platyrhynchos* Valenciennes, 1840a.Yet the species' status is unresolved, as those opinions apparently were based on examination of a specimen which was incorrectly thought to be the type (C. Ferraris pers. comm.), and Lichtenstein's specimen has not been located. Marceniuk and Ferraris Jr (2003) placed the species in the synonymy of *Bagre bagre* (Linnaeus) based on Lichtenstein's description.

Tachysurus Lacépède, 1803

Tachysurus Lacépède, 1803:150 (type species *Tachysurus sinensis* Lacépède 1803. Type by monotypy).

Wheeler and Baddokwaya (1981) discussed the status of *Tachysurus* Lacépède and concluded that the painting on which the description is based is not of an ariid but of a siluroid fish from fresh waters of China. Lacépède's genus *Tachysurus* (and *Tachysurus sinensis*) therefore is a nomen dubium.

The following observations are relevant: (1) the fish depicted by Lacépède probably belongs to a species of *Pelteobagrus* (Bagridae) (M. Kottelat, pers. comm.); (2) an ariid commonly identified as *Arius sinensis* (non Lacépède) occurs in the East and South China Sea (see also Fowler 1932). It is figured and described by Chu *et al.* (1999). I have re-identified a specimen identified as that species by Fumio Ohe (Bihoku High School, Aichi Prefecture, Japan) as *Arius arenarius* (Müller and Troschel). It is possible that the species called *Arius sinensis* by Mai (1978) is also referable to *A. arenarius*. Kottelat (2001) also re-identified *Arius fangi* Chaux in Chaux and Fang, 1949, from Vietnamese waters as *A. arenarius*.

Arius arenarius is most similar to *A. arius* (Hamilton), which also occurs in the area. *Arius arius* is a senior synonym of *Arius falcarius* Richardson, a species placed in the synonymy of *Arius sinensis* (non Lacépède) by Chu *et al.* (1999) and earlier authors (Eschmeyer 1998, 2003). The main distinguishing characters are identified in Table 3.

Incertae sedae

Several taxa, about which usually I had sound information, cannot be accommodated into the proposed classification. Further study should reveal the appropriate placement for these taxa.

Genidens Castelnau, 1855

Genidens Castelnau, 1855: 33 (type species *Bagrus genidens* Valenciennes, 1840. Type by original designation, or by absolute tautonomy). Synonyms from literature: *Genidens cuvieri* Castelnau, 1855; *Genidens granulosus* Castelnau, 1855.

Genidens is characterised by the low conical palate teeth embedded on two extensive, thick 'cushions', one on each side of the palate. Sometimes there is more than one tooth patch on each side of the palate; there are no vomer teeth. The lower jaw symphysis is upturned, the mouth is small, and there is a prominent median ridge on the palate. The gill openings are slightly restricted, and the lower inside of the operculum bears a deep pouch. The chin barbels have

Table 3. Characters separating *Arius arius* (Hamilton) and *Arius arenarius* (Müller and Troschel).

	mx barbel as % of SL	eye diameter in head length	eye diameter in snout length	dorsal fin filament in adult	adipose fin with dark spot	tooth patches on palate
arius	24–37	4–6	about 2	yes	yes	spreading from front to back
arenarius	15–24	6–8	about 3	no	no	at front only

membranous inner margins. The posterior cleithral process, and the adipose fin base, are short. The mesethmoid is notched and extends ventrally to reduce the lateral ethmoid-frontal space; the posterior dorsomedian fontanelle is absent; the temporal fossa is open; and the subvertebral cone is moderately high. The Mullerian ramus is high and strongly curved and the flange of the fourth neural spine is broad. The fourth and fifth parapophyses are turned at right angles, the fifth one long and expanded distally; the posterior margin of the laminar bone over the anterior vertebrae is raised distally.

Br 6. A 16–19. P. I,10. Total gill rakers (first arch) 14–16. Vertebrae 7+11+5+28.

Comparisons. In the phylogenetic analyses (this work; Kailola 1990) *Genidens* always separated out near *Brustiarius*, *Ariopsis*, *Ariodes* and *Arius* (Fig. 15). *Genidens genidens* has features in common with *Brustiarius*, such as acute posterior cleithral process (*B. nox*), large eye, variable development of palate teeth and poorly developed buccopharyngeal pads (like *B. solidus*); but it differs in having a somewhat restricted gill opening, pale mouth cavity, a deeply notched mesethmoid, straight nasal bone, moderately long hyomandibular-metapterygoid sutures, rugose skull surface, no teeth on the vomer and rakers absent only occasionally from the back of the first gill arch.

Genidens bears several character-states that are either homoplastic (e.g., dentition, short posterior cleithral process) or autapomorphic (e.g., the expanded fifth parapophysis). Marceniuk and Ferraris Jr (2003) regarded it as a senior synonym of *Guiritinga* Bleeker (see below).

Distribution. Freshwaters of north-eastern South America.

Guiritinga Bleeker, 1858

Guiritinga Bleeker, 1858: 62, 67 (type species *Pimelodus commersonii* Lacépède, 1803. Type by monotypy).

See comments under *Ariopsis*, above.

In *Guiritinga barbus* (the senior synonym of *Pimelodus commersonii*), the lower inside of the operculum bears a deep pocket or pouch and the gill membrane is broadly attached to the lower inside operculum. A deep pocket on the inside of the operculum is present also in *Osteogeneiosus*, *Galeichthys* and *Genidens*. The temporal fossa is almost absent and the metapterygoid hind margin is in line with the hind margin of the quadrate. The laminar shelf bears a deep pocket on each side of the central ridge (a feature also present in *Cinetodus froggatti*, some *Sciades* species and *Nedystoma dayi*) and the peritoneum is dusky brown or spotted (also in *Hexanematichthys sagor* and *Arius oetik*).

In *Guiritinga* the palatal dentition sometimes breaks into patches on each side (as also in *Genidens* and cf. *Arius harmandi*). In *G. planifrons* the bases of the fourth to sixth transverse processes are exposed, and the laminar bone is deeply excavated.

Distribution. Eastern South America. Inshore waters.

Taxa. *Guiritinga barbus* Lacépède, 1803 (synonym: *Pimelodus commersonii* Lacépède, 1803); *G. planifrons* (Higuchi, Reis and Araujo, 1982).

cf. *Arius rugispinis* Valenciennes, 1840a, and cf. *Arius phrygiatus* Valenciennes, 1840a

Synonym from literature for cf. *Arius rugispinis*: *Tachysurus atroplumbeus* Fowler, 1931; synonym from literature for cf. *Arius phrygiatus*: *Arius dieperinki* Bleeker, 1862a.

These taxa appear distinct by the combination of their tapered head, very rugose and granular head shield confined to the distal half of the head, long dorsomedian fontanelle, triangular and ridged supraoccipital process, small eye (10–14 in head length) and very long adipose fin (longer than anal fin base). The mouth is somewhat inferior, the lips are thick, the maxillary tooth band is broad and emarginate at each end. There are low and conical teeth in two small widely spaced patches on the palate. The gill openings are wide, there are 13–17 gill rakers on the first gill arch, and there are no rakers along the back of the first two gill arches; the barbels are thin, and the bases of the chin barbels are aligned. The lateral line is much branched, the humeral process is granular, the axillary pore is minute and the fin spines are broad. The mesethmoid has a deep median notch and short cornuae; the frontal is narrow anteriorly with long thin arms, the space between them and the triangular lateral ethmoid is large. The long alary processes (off the parasphenoid) extend across the space to touch the frontal arms. The subvertebral cone is high and the posteromedian flange of the epioccipital and lamina of the fourth neural spine are high and strong. The laminar bone over the fused vertebrae is extensive, the temporal fossa is large, the vomer is 'T'-shaped, and the epioccipital abuts but does not enter the skull roof.

Comparisons. These taxa appear to have affinity with *Cathorops* by their tapered head, short-armed and notched mesethmoid, large frontal-mesethmoid space, extensive laminar bone and high subvertebral cone, but they differ because of (for example) the epioccipital feature and absence of posterior gill rakers.

Distribution. North-eastern South America. Estuaries and inshore marine waters.

cf. *Arius acutirostris* Day, 1877

Chandy (1953: 3) stated: 'This is one of the species recorded by Day from the fresh waters of Burma, where it is commonly found. The species is easily identified on account of its pointed rostrum, from which the specific name is derived. The rostrum is formed by the elongation of the upper jaw which is fleshy and lies in advance of the lower jaw.' I have examined whole material (Appendix A) and add the following information: the buccopharyngeal ornamenture is well-developed; rakers are present along the back of all gill arches; the fins are pigmented and the rugose dorsal spine may be chambered; the eye is situated dorsolaterally, and its margin is not completely free; the barbels are thin and short, the chin barbel bases are aligned; the jaw teeth are long and depressible and the low and conical palate teeth form two ovate patches at the front of the palate.

Distribution. Burma. Fresh water.

cf. *Arius harmandi* (Sauvage, 1880a)

Probable synonym: *Arius brevirostris* Steindachner, 1901.

I have redescribed the type material (Kailola 1999). The species is distinguished by its striated head shield, slender jaw teeth, conical palate teeth arranged into four patches forming a wide crescent across the front of the palate, and rakers along the back of all gill arches.

Distribution. Thailand to Borneo. Estuaries and tidal reaches of rivers.

cf. *Arius macrorhynchus* (Weber, 1913)

Synonym*: Hemipimelodus aaldereni* Hardenberg, 1936.

The appropriate position for this species was not found in the phylogenetic analyses, although it was consistently nearest the *Plicofollis* clade (Fig. 15) and *Genidens*. The species cf. *Arius macrorhynchus* is characterised by a mesethmoid which is convex, heavily striated with short cornuae and turned ventrad, a uniquely shaped nasal bone and angular lachrimal, short metapterygoid-hyomandibular suture, large temporal fossa, frontal bone broad posteriorly with narrow anterior arms, laminar bone over the anterior vertebrae reduced, long barbels rounded in cross-section, small ventral mouth and prominent snout indented at the nostrils, lips present only at the mouth corners, mouth small and inferior, no teeth on the palate, no rakers along the back of the first gill arch, and a short-based adipose fin.

Br 7. A 20–22. P. 1,10–11. Total gill rakers (first arch) 12–15. Vertebrae 17+5–6+28–29.

Distribution. Central-southern New Guinea. Fresh water.

Specimens of an unknown species collected by Maurice Kottelat in 1991 from a freshwater lake in the Mahakam River basin in eastern Borneo appear to belong in the same group as does cf. *Arius macrorhynchus*.

cf. *Arius subrostratus* Valenciennes, 1840a

Synonym from literature (Day 1877): *Arius rostratus* Valenciennes, 1840a.

Chandy (1953: 13) stated: 'This is an exclusive peninsula species of India ... It is a marine form, ascending rivers. ... The species has a remarkably long dorsal filament, reaching adipose fish [sic].' The head is 'dog'-like and the mouth is small; the large eye is dorsolateral; the barbels are short, the maxillary barbel reaching only as far as the eye, or less; the short conical palate teeth are in two widely separated oval patches; rakers are present on the back of all gill arches and the buccopharyngeal pads are well developed; the gill openings are partly restricted; the fin spines are strong, the dorsal spine bearing a filament; the lateral line bifurcates at the tail base, and the caudal fin lobes are broad. The inner rays of the pelvic fins are thickened in mature females. Total gill rakers (first arch) 22–26; A. 18–19.

Distribution. Pakistan and India. Jayaram (1982) reported that the species is found as far east as Philippines and Indonesia but according to other authors (Weber and de Beaufort 1913; Herre 1926; Kottelat *et al.* 1993; Tan and Ng 2000) this is not so.

West African taxa. (refer Taylor and van Dyke 1981; Taylor 1986).

Lacking access to appropriate material and other resources, I am unable to suggest the appropriate placement for the ariid fauna of West Africa. Taylor and van Dyke (1981) and Taylor (1986) recorded five species from the region: *Arius africanus* Günther in Playfair and Günther, 1867; *Arius gigas* Boulenger, 1911; *Arius heudelotii* Valenciennes, 1840a; *Arius latiscutatus* Günther, 1864; *Arius parkii* Günther, 1864.

CONCLUSIONS

The findings from this study lay the foundations for a much better and respectable global understanding of ariid catfish systematics, despite problems involved in hypothesising the phylogeny of some sections of the family through my lack of access to material. In addition, because it is the most widely-dispersed catfish family (extant or extinct representatives known from five of the six continents) and tolerates a variety of water habitats, the phylogenetic information revealed here will facilitate the development of hypotheses of comparative evolution and zoogeography of the entire Otophysi clade of ostariophysans (Fink and Fink 1996).

The Ariidae was long regarded as a pariah among siluroid families (Gosline 1975) – a status quite clearly undeserved. As discussed earlier, the play of homoplasy is remarkable and the selection of characters has been a challenge; yet even relatively generalised catfishes (ariids, sisorids: Roberts and Ferraris Jr 1998) have highly specialised features. It may be that other researchers will choose different characters and outgroups (and have available more material) and the relationships of those characters may lead those researchers to re-state genera and re-align contained species; for example, Markle (1989) arrived at different character polarity in gadoid fishes through the use of alternative outgroups. Even so, I believe that combinations of many of the characters I have used here identify natural suites of ariid taxa and that the phylogeny I presented here reflects true relationships.

Warts and all, this presentation is made to lay a more informed foundation for the resolution of ariid phylogeny and systematics. From one perspective, it's all a matter of balance, and from the other, they're all pretty marvellous fish.

ACKNOWLEDGMENTS

Telling this story, after 13 years, seemed such an enormous task especially as I live and work in Pacific countries where required resources do not exist (e.g., the time between manuscript submission and publication has taken more than three years). But encouraging noises from friendly ichthyologists have kept me going. Helen Larson (NTM) particularly, has been determined to get the show-on-the-road: she assisted with literature citations, a second PAUP analysis, and preparation of figures. Helen's assistance has been invaluable. Chris Glasby (NTM), Mark McGrouther and Jeff Leis (AMS) have generously supported my efforts also. Carl Ferraris Jr (CAS) provided helpful comment on an earlier draft of the manuscript and assisted with information on South American ariids, and the later assault of two reviewers turned ramblings into reasonableness. Heok Hee Ng (UMMZ), Maurice Kottelat (Switzerland), Tony Gill (previously BMNH) and Bill Eschmeyer (CAS) provided information on particularly species. Julie Easton (Bureau of Rural Sciences, Canberra) assisted by drafting earlier figures which were redrawn by Sue Dibbs (NTM). So many people gave me information on catfishes, lent me material, and otherwise supported my study up until 1990, and recently: thanks to all of you, especially the senior curators and collection managers of ichthyological collections worldwide. Access more recently to material made available by Kent Hortle (previously Freeport Mining Ltd, West Papua, Indonesia) and Fumio Ohe (Japan) has been useful. The 1980s staff of the Zoology Department, University of Adelaide are acknowledged and chief among them is my PhD supervisor, Professor Michael Tyler. Although my study was 'only' on the Sahul Shelf ariids, Mike reluctantly turned a blind eye to my borrowing of material from far and wide – perhaps not wide enough – before he eventually put his foot down; else I'd never have submitted my dissertation! My family of course: drums of catfish around the home for years ... Like the families of all studiers-of-fishes, mine was long-suffering and supportive.

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Accepted 1 March 2004

APPENDIX A. Ariid material examined. Species names are those given in their original descriptions. Asterisks indicate specimens examined more thoroughly.

***Arius aerocephalus* Weber, 1913** – 1, AMNH 9514, Lorentz River, southern New Guinea, 120 mm SL, paratype*.

***Arius acutirostris* Day, 1877** – 1, AMS B.7733, Irrawaddy River, Burma, Day's Collection, 82 mm SL*; 5, NHRM MAL/1934.457.3513, Moulmein, Burma, 107–132 mm SL*.

***Arius acutus* Bleeker, 1846** – 5, (possibly including syntype(s): Kailola 1990), RMNH 6895 (in part), East Indies Archipelago, 150–260 mm SL*.

***Ariodes aeneus* Sauvage, 1883** – 2*, MNHN A.5155, "Iles Raffles" (=Singapore), 113–117 mm SL, cotypes*.

***Arius andamanensis* Day, 1871** – 1*, ZSI 1307, Andaman Islands, 246 mm SL, cotype*; 1, AMS B.7931, Andaman Islands, 192 mm SL, cotype (type status confirmed: Ferraris Jr et al. 2000)*.

***Galeichthys aquadulce* Meek, 1904** – 1, UMMZ 197272, 160 mm SL; 2, UMMZ 198711, 212–231 mm SL (skeletons)*; 1, UMMZ 198712, 234 mm SL (skeleton)*; 6, UMMZ 143454, Guatemala, 105–205 mm SL*.

***Arius arenarius* Müller and Troschel, 1849** – 1, ZMB 3001, China, 255 mm SL, holotype*; 3, USNM 191247, Tanshui, Taipei Hsien, Taiwan, 217–250 mm SL*; 1, CAS SU 27967, Hong Kong, 240 mm SL; 1, USNM 191246, Taiwan, 220 mm SL; 1, MCZ 23717, China, 172 mm SL; 1, USNM 86363, China, 123 mm SL; 13, USNM 86932, Foochow, China, 72–166 mm SL; 2, USNM 86345, China, 53–58 mm SL; 1, USNM 87096, Hainan, 97 mm SL; 1, ANSP 52670, China, 290 mm SL; 1, ANSP 76603, Hong Kong, 207 mm SL; 1, ANSP106773, Fukien, China, 69 mm SL; 2, CAS SU30273, Canton, 73–83 mm SL; 1, CAS SU26967, Hong Kong, 240 mm SL; 3, CAS SU1764, Swatow, China, 63–91 mm SL; 1, CAS SU35777, 111 mm SL; CAS SU2796, Tinghai, Chusan Island, 85 mm SL; 3, MCZ 7714 (part), Penang, Malaysia, SL not recorded; 1, CSIRO H.5299-01, 80 kilometres off Xiangshan, East China Sea, 290 mm SL. **(= type species of *Ariodes* Müller and Troschel).**

***Arius argyropleuron* Valenciennes, 1840** – 48 specimens examined (Kailola 1990) from India (Bombay), Malaysia (Penang), Java, southern New Guinea to northern Australia (Dampier to Moreton Bay). **(= type species of *Plicofollis* n. gen.).**

***Pimelodus arius* Hamilton, 1822** – 1, LACMNH 38126–27, Karachi fish market, Pakistan, 176 mm SL*; 6, LACMNH 38129–95, off mouth of Korangi Creek, Sind, Pakistan, 99–190 mm SL *; 1, LACMNH 38132-63 (in part), mouth of Turshian Creek, Sind, Pakistan, 83 mm SL*; 1, LACMNH 38134–52, about 6 miles south of Hajambro Creek, Sind, Pakistan, 188 mm SL*; 1, LACMNH 38135–35, lower 10 kilometres of Hajambro Creek, Sind, Pakistan, 243 mm SL*; 1, NMV 45949, East Indies Archipelago, Bleeker Collection A, 156 mm SL; 1, NMV 20620, 'Island of Formosa', 153 mm SL; 2, USNM 248196, Sind River, Hyderabad, Pakistan, 200–220 mm SL; 5, RMNH6899, no collection data, coll. P. Bleeker, 161–271 mm SL, paratypes of *Pseudarius arius**; 1, AMS I.28082-041 (part), Malaysia, 123 mm SL. **(= type species of *Arius* Valenciennes and *Pseudarius* Bleeker).**

***Arius armiger* de Vis, 1884** – 206 specimens examined (Kailola 1990) including the syntypes (QM I.3088, 148 mm SL; QM I.3089, 134 mm SL)* from localities ranging from southern New Guinea (Vogelkopf Peninsular to Yule Island) to northern Australia (King River to eastern Gulf of Carpentaria). **(= type species of *Nemapteryx* Ogilby, based on *stirlingi* Ogilby, a junior synonym of *armiger* De Vis).**

***Arius assimilis* Günther, 1864** – 1, GCRL V70:4657, Quintana Roo, Mexico, 87 mm SL*; 1, UMMZ 197184, Guatemala, 320 mm SL (skeleton)*; 2, LACMNH, Rio Chiuaha, Honduras, 76–80 mm SL*; 3, GCRL V70:6008, Boca del Rio Chibana, Honduras, 42–85 mm SL*.

***Hemipimelodus atripinnis* Fowler, 1937** – 1, ANSP 67096, Bangkok, Thailand, 130 mm SL, type*.

***Arius augustus* Roberts, 1978** – 15 specimens examined (Kailola 1990) including types (AMS I.27090-001, 342 mm SL, holotype; AMS I.22460-001, 308 mm SL, paratype; KFRS F.4681-01, 285 mm SL, paratype; USNM 217068, 2 specimens, 90–101 mm SL; USNM 217067, 412 mm SL paratype)* from localities ranging from the upper Fly River to the Vailala River, southern New Guinea.

***Arius australis* Günther, 1867** – 1, BMNH 1866.6.19.7, Hunter River, eastern Australia, 380 mm SL, syntype*; 1, BMNH 1866.2.13:4, same data, 275 mm SL, syntype*.

***Galeichthys azureus* Jordan and Williams, in Jordan, 1895** – 1, CAS SU 11575, Mexico, 392 mm SL, holotype*.

***Silurus bagre* Linnaeus, 1766** – 1, GCRL V81:17228, 04°41'S, 51°16'W, 193 mm SL*; 1, CAS 27063, skull, 58 mm HL. **(= type species of *Bagre* Cloquet).**

***Pimelodus barbus* Lacépède, 1803** – 1, GCRL unregistered, 32°58'S, 52°27'W, 179 mm SL*; 1, unregistered, Rio Grande, Mexico (skeleton)*. **(= type species of *Guiritinga* Bleeker, based on *Pimelodus commersonii* Lacépède, a junior synonym of *barbus* Lacépède).**

***Tachysurus (Pararius) berneyi* Whitley, 1941** – 94 specimens examined (Kailola 1990) including types (AMS I.13076, 141 mm SL, type; AMS I.13075, 255 mm SL, paratype; 12 specimens, AMS I.8077 – AMS I.8088, 79–116 mm SL, paratypes)* from localities between the Fly and Strickland River systems, southern New Guinea and rivers draining northwards into the Gulf of Carpentaria, northern Australia.

***Hemipimelodus bernhardi* Nichols, 1940** – 3, AMNH 15040, Bernhard Camp, Idenberg River, New Guinea, 109–173 mm SL, paratypes*.

***Hemipimelodus bicolor* Fowler, 1935** – 1, ANSP 60777, Bangkok, Thailand, 190 mm SL, type*.

***Bagrus bilineatus* Valenciennes, 1840** – 214 specimens examined (Kailola 1990) including a cotype (MNHN A.9344, 240 mm SL)* from localities between the north-western Indian Ocean (Bahrain; Arabia) to eastern Australia (Townsville).

***Arius bleekeri* Popta, 1900** – 2, RMNH 6825, no collection data, but probably East Indies Archipelago, 114–124 mm SL, types*.

***Arius boakeii* Turner, 1867** – 1, BMNH 1866.7.11:1, Ceylon, 163 mm SL, type*.

***Pimelodus borneensis* Bleeker, 1851** – 1, RMNH 27618, Bandjermassin, Borneo, 113 mm SL, type (also a syntype of *Hemipimelodus macrocephalus* Bleeker, 1858: M. Boeseman, in litt.)*; 1, NMV 46464, East Indies Archipelago, Bleeker Collection A, 82 mm SL*; 1, ANSP 60710-15, Bangkok, Thailand, 106 mm SL*; 5, UMMZ 181175, Tonle Sap, Mekong River drainage, Cambodia, 98–128 mm SL*; 1, UMMZ 214631, Chau Doc market, Vietnam, 120 mm SL; 2, UMMZ 214645, Chau Doc market, 130–144 mm SL; 1, USNM 103195, Thailand, 175 mm SL; 2, ANSP 87374, Bangkok, Thailand, 130–144 mm SL; 5, ANSP 60710-16 (part), 33–106 mm SL; 1, UMMZ V74-173, Vietnam, 32 mm SL; ?, UMMZ V74-179, Vietnam, 31–40 mm SL; 1, UMMZ V74-174, Vietnam, 34 mm SL; 13, UMMZ V74-171, Vietnam, 31–45 mm SL. **(= type species of *Hemipimelodus* Bleeker).**

***Ancharius brevibarbis* Boulenger, 1911** – 2, MNHN 1960-235, Règion de l'Est, freshwater, Madagascar, 119 –173 mm SL.

***Tachysurus broadbenti* Ogilby, 1908** – 1, QM I.9745, Cape York, Queensland, 290 mm SL, syntype*.

***Arius burmanicus* Day, 1870** – 1, AMS B.7520, Moulmein, Burma, 265 mm SL, syntype* (type status confirmed: Ferraris Jr et al. 2000); 1, NHRM Mal/1934-457 3512, Moulmein, Burma, 163 mm SL*; 1, MCZ 7297, 265 mm SL*.

***Arius caelatus* Valenciennes, 1840** – 1, MNHN B.589, Batavia, Java, 260 mm SL, type*; 1, QM I.24783, Tanjung Priok, Jakarta, 1980, 295 mm SL*; 1, AMS I.26979-001, Muarakarang, Jakarta, 1980, 129 mm SL*; 1, AMS I.26979-002, same data, 198 mm SL*; 3, AMS I.26979-003, same data, 206–229 mm SL*; 1, QM I.25784, same data, SL not recorded; 1, MZB 2160, Belukang, Lampung Selatan, 154 mm SL*; 1, AMS B.7940, Bombay, India, Day's Collection, approx. 290 mm SL*; 61, LACMNH 60649-89, Bangkok, Thailand, 37–62 mm SL; 1, ANSP 77914, Bangkok, Thailand, 207 mm SL; 1, ANSP 60716, Thailand, 45 mm SL; 1, ANSP 77240, Saigon, Vietnam, 108 mm SL; 4, ANSP 61573–77 (part), Thailand, 47–59 mm SL; 13, ANSP 60690-702, Bangkok, Thailand, 1934, 63–134 mm SL; 3, ANSP 61568–72, Bangkok, Thailand, 40–56 mm SL; 1, LACMNH 38128–47, 194 mm SL*; 1, ANSP 61599, Bangkok, Thailand, 81 mm SL; 1, ANSP 60735–36 (part), Paknam, Thailand, 125 mm SL; 1, NMV 45986, East Indies Archipelago, no date, Bleeker Collection A, SL not recorded; 1, AMS I.27635-003, Malaysia, 165 mm SL.

***Arius caerulescens* Günther, 1864** – 22, LACMNH 32295-2, 42–143 mm SL*.

***Bagrus carchariorhynchos* Bleeker, 1846** – 2, RMNH 6885 (in part), Batavia, 137–370 mm SL*, larger specimen probably the type (Kailola 1990).

***Arius (Hemiarius) carinatus* Weber, 1913** – 19 specimens examined (Kailola 1990) including five syntypes (ZMA 111.110, 155 mm SL; AMNH 9265, 2 specimens, 50–50 mm SL; RMNH 28007, 212 mm SL; MZB 143, 2 specimens, 80–90 mm SL)* from localities between the Sande River and Lakekamu River, southern New Guinea.

***Arius cleptolepis* Roberts, 1978** – 1, USNM 217070, upper Fly River, southern New Guinea, 218 mm SL, paratype*; 1, USNM 217071, downstream from Kiunga, southern New Guinea, 353 mm SL, paratype*.

***Arius coatesi* Kailola, 1990** – 9 specimens examined (Kailola 1990a) including types (AMS I.25405-001, 270 mm SL (holotype); AMS I.25405-002, 450 mm SL; KFRS FO3995, 237 mm SL; KFRS FO4018, 242 mm SL; QM I.21673, 375 mm SL; WAM P.28221-001, 4 specimens, 290–390 mm SL)* from localities in the Sepik and Ramu rivers, northern New Guinea.

***Hemipimelodus cochlearis* Fowler, 1935** – 1, ANSP 60767, Paknam, Thailand, 160 mm SL, holotype; 6, ANSP 60768-60773, Paknam, Thailand, 137–156 mm SL, paratypes*.

***Hemipimelodus colcloughi* Ogilby, 1910** – 1, QM I.1538, Croker Island, Northern Territory, 158 mm SL, type*.

***Tetranesodon conorhynchus* Weber, 1913** – 1, ZMA 111.084, Lorentz River, southern New Guinea, 170mm SL, holotype*. **(= type species of *Tetranesodon* Weber).**

***Bagrus couma* Valenciennes, 1840** – 1, MCZ 51717, Georgetown, Guyana, 197 mm SL*; 2, UMMZ 201601-S (skeletons)* (this material is catalogued as *Arius kessleri* Steindachner).

***Hemipimelodus crassilabris* Ramsay and Ogilby, 1886** – 11 specimens examined (Kailola 1990) including types (AMS B.9961, 161 mm SL (holotype); QM I.857, 127 mm SL)* from localities from the Digoel River to the Purari River, southern New Guinea. **(= type species of *Pachyula* Ogilby).**

***Arius crossocheilos* Bleeker, 1846** – 3, RMNH 6894, 'East Indies', 155–297 mm SL, syntypes*; 1, MCZ 24861, 143 mm SL.

***Arius curtisii* Castelnau, 1878** – 1*, MNHN B.693, Moreton Bay, eastern Australia,144 mm SL, syntype*. **(= type species of *Neoarius* Castelnau).**

***Arius (Hemiarius) danielsi* Regan, 1908** – 18 specimens examined (Kailola 1990) including the holotype (BMNH 1905.8.15:21, 148 mm SL)* from localities ranging from the Lorentz River system to the Purari River system, southern New Guinea.

***Arius dasycephalus* Günther, 1864** – 1, BMNH 1855.9.19:1100, 'Oahu, Hawaii', Haslar collection, 229 mm SL, holotype*; 1, AMS I.4981, Panama, 220 mm SL*.

***Hemipimelodus dayi* Ramsay and Ogilby, 1886** – 29 specimens examined (Kailola 1990) including types (AMS B.9938, 162 mm SL, holotype; AMS B.9939, 112 mm SL, paratype; AMS B.9940, 166 mm SL, paratype; AMS B.9942, 162 mm SL, paratype; QM I.879, 3 specimens, 75–161 mm SL, paratypes)* from localities from the Lorentz River to the Purari River system, southern New Guinea. **(= type species of *Nedystoma* Ogilby).**

***Arius dioetes* Kailola, 2000** – 26 specimens examined (Kailola 2000) including types (CSIRO C.3798, 430 mm SL, type; NTM S.11190-001, 2 specimens, 450–460 mm SL, paratypes; AMS I.15557-041, 2 specimens, 103–172 mm SL, paratypes; AMS I.29292-001, 159 mm SL, paratype; CSIRO H.5154-01, 1050 mm SL, paratype; NTM S.14828–005, 95.1 mm SL, paratype; KFRS FO4094, 200 mm SL, paratype)* from localities ranging from the Kamora River to Oreke River in southern New Guinea and Adelaide River to Norman River, northern Australia.

***Arius dispar* Herre, 1926** – 4, AMS I.37418-001, Dau market, Manila, Philippines, 176–231 mm SL*; 2, NSMT P.43697 (part), East China Sea (32°35'N, 122°40'E), 157–177 mm SL*; 1, CAS SU 35081, Los Banos, Philippines (skeleton)*; 1, USNM 78097, Los Banos, Philippines, 93 mm SL; 1, unreg?, Philippines, 88 mm SL*.

***Leptarius dowii* Gill, 1863** – 1, CAS SU 5548, Panama, 284 mm HL (skeleton)*; 1, USNM 214859, 125 mm HL (skeleton)*. **(= type species of *Leptarius* Gill)** .

***Arius dussumieri* Valenciennes, 1840** – 1, AMS B.8013, Malabar, India, Day's Collection, 111 mm SL*; 1, SAM 12381, Chinoe River, Africa, 187 mm SL*; 1, SAM 12403, Chinoe Ocean Beach, Africa, 163 mm SL*; 3, LACMNH 38131-48, Hajambro Creek mouth, Sind, Pakistan, 145–163 mm SL; 1, USNM 297919, Visakhapatnam, India, 186 mm SL; 1, USNM 160551-53?, Philippines, SL not recorded; 6, AMS I.28123-001, Mozambique, 115–137 mm SL.

Galeichthys eigenmanni **Gilbert and Starks, 1904** – 3, CAS SU 12878, 12879, 12880 (3 lots), 240–295 mm SL, paratypes; 1, CAS SU 6987, no data, 276 mm SL, holotype*.

Tachysurus eumelane **Gilbert in Jordan and Evermann, 1898** – 1, CAS SU 5818, Panama, 231 mm SL, holotype*.

Bagrus (Sciades) emphysetus **Müller and Troschel, 1849** – 1, ZMB 2990, Surinam, 320 mm SL, holotype*. **(= type species of *Sciades* Müller and Troschel and *Sciadeichthys* Bleeker)**

Tachysurus evermanni **Gilbert and Starks 1904** – 1, CAS SU 6706, Gulf of Panama, 206 mm SL, holotype*.

Arius falcarius **Richardson, 1845** – 1, AMS B.7943, Bombay, India, Day's Collection, 258 mm SL*.

Galeichthys feliceps **Valenciennes, 1840** – 1, SAM 23981, Strandfontein, South Africa, 93 mm SL*; 3, SAM 25000, no data, 138–171 mm SL*; 2, AMS I.19799-002, Knysa, South Africa, 39–42 mm SL; 1, AMS I.37513-001, South Africa, 290 mm SL*; 1, AMS I.29287-001, South Africa, 280 mm SL; 1, USNM 292844, 33° 39'20"S, 26° 44'E, 300 mm SL (skeleton)*. **(= type species of *Galeichthys* Valenciennes).**

Silurus felis **Linnaeus, 1766** – 1, MCZ 31925, Beaufort, North Carolina, America, 216 mm SL*; 1, GCRL V71:7705, Lemon Bay, Florida, 205 mm SL; 1, LACMNH 32600-1, c. 275 mm SL (skeleton)*; 1, UMMZ 18641-S, Mexico, 300 mm SL (skeleton); 1, UMMZ 17947, 322 mm SL (skeleton); 1, UMMZ 186995-S, 322 mm SL (skeleton)*; 1, UMMZ 186481, 290 mm SL (skeleton); 1, GCRL V62:652, Mississippi Sound, America, 110 mm SL; 1, LACMNH 32705–3, 134 mm SL*; 5, ZMB 31872, Biloxi, Mississippi, east of Ship Island, SLs not recorded; 18, AMS I.28768-001, same data, 130–150 mm SL; 7, AMS I.37417-001, same data, 55–265 mm SL. **(= type species of *Ariopsis* Gill, based on *Arius milberti* Valenciennes, a junior synonym of *felis* Linnaeus).**

Arius froggatti **Ramsay and Ogilby, 1886** – 28 specimens examined (Kailola 1990) including holotype (AMS B.9936, 244 mm SL)* from localities ranging between the Digoel River to Kerema Bay in southern New Guinea and the Roper River system and coast, northern Australia. **(= type species of *Cinetodus* Ogilby).**

Arius fuerthii **Steindachner, 1877** – 2, GCRL V79:16684, Jiquilisco Bay, El Salvador, 157–159 mm SL; 3, GCRL V79:16699, same data, 136–160 mm SL; 1, GCRL V79:16693, same data, 170 mm SL; 1, LACMNH 31310-27, Panama, 193 mm SL*; 25, GCRL V79: 16688, EL Salvador, 115–148 mm SL*.

Ancharius fuscus **Steindachner, 1880** – 3, NMHN1966-897, Madagascar, freshwater, 100–140 mm SL. **(= type species of *Ancharius* Steindachner).**

Pimelodus gagora **Hamilton, 1822** – 1, AMS B.7706, Calcutta, India, Day's Collection, 192 mm SL*; 1, ANSP 87532, Bombay, 154 mm SL; 4, CAS SU 33795, Rangoon, Burma, 110–208 mm SL; 2, UMMZ 208352, Bangladesh, 122–137 mm SL; 2, UMMZ V74-172, Vietnam, 110–121 mm SL; 1, UMMZ V74-171, Vietnam, 81 mm SL; 1, UMMZ V74-57, Vietnam, 123 mm SL.

Bagrus genidens **Valenciennes, 1840** – 1, AMS I.2630, Brazil, 149 mm SL*; 4, MCZ 27275, no data, 122–181 mm SL; 4, ANSP 121228, Brazil, 85–97 mm SL; 2, ANSP 121581, Brazil, 115–223 mm SL; 1, MCZ no number, Rio de Janeiro (skeleton). **(= type species of *Genidens* Castelnau).**

Galeichthys gilberti **Jordan and Williams, in Jordan, 1895** – 4, CAS SU 11666, 11667*, 11668 (3 lots), Sinaloa, Mexico, 163–280 mm SL, paratypes; 1, LACMNH W58-36, no data, 228 mm SL, holotype?*.

Tachysurus (Pararius) godfreyi **Whitley, 1941** – 1, AMS I.5270, Port Darwin, 305 mm SL, holotype*.

Arius goniaspis **Bleeker, 1858** – 1, BMNH 1863.12.11:159, Sumatra, 73 mm SL, syntype*.

Arius graeffei **Kner and Steindachner, 1866** – 453 specimens examined (Kailola 1990) including the holotype (NMW 67 152, 253 mm SL)* from localities between Jamoer Lake and Goldie River, southern New Guinea, and the Abrolhos Islands (western Australia) to the Hunter River (eastern Australia)

Arius grandicassis **Valenciennes, 1840** – 1, USNM, 214876, HL 90 mm (skeleton)*; 3, GCRL V81:17226 (in part), Surinam, 156–237 mm SL. **(= type species of *Notarius* Gill)**

Arius guatemalensis **Günther, 1864** – 5, GCRL V71:6501, Oxaca, Mexico, 55–130 mm SL*; 1, GCRL V70:5021, El Salvador, 50 mm SL*.

Arius hainesi **Kailola, 2000** – 34 specimens examined (Kailola 2000) including types (NTM S.11507-001, 304 mm SL, holotype; AMS I.25995–001, 204 mm SL, paratype; QM I.22657, 228 mm SL, paratype; AMS I.27414-001, 237 mm SL, paratype; USNM 288553, 135 mm SL, paratype; AMS I.25996-001, 136 mm SL, paratype; CSIRO C.3799, 187 mm SL, paratype; NTM S.10190-002, 2 specimens, 88–88 mm SL, paratypes; CSIRO H.4545-01, 2 specimens, 120–126 mm SL, paratypes; CSIRO H.4937-03, 223 mm SL, paratype; CSIRO H.5252-01, 2 specimens, 210–234 mm SL, paratypes)* from localities from the Kamora River to Oreke River in southern New Guinea and Darwin to the Gulf of Carpentaria in northern Australia. **(= type species of *Amissidens* n. gen.).**

Arius hamiltonis **Bleeker, 1846** – 5, (possibly including syntype(s): Kailola 1990), RMNH 6895 (in part), East Indies Archipelago, 150–260 mm SL*.

Arius hardenbergi **Kailola, 2000** – 6 specimens examined (Kailola 2000) including types (WAM P.29966-001, 260 mm SL, holotype; NCIP 436, 254 mm SL, paratype; AMS I.29291-001, 2 specimens, 60–75 mm SL, paratypes; QM I.26088, 56 mm SL, paratype)* from localities between the Vogelkopf Peninsular and Fly River mouth, southern New Guinea.

Hemiarius harmandi **Sauvage, 1880a** – 1, MNHN 2390, Ile de Phu-Quoc (Gulf of Siam), 122 mm SL, holotype*.

Hexanematichthys henni **Eigenmann, 1922** - 3, CAS SU60620, Ecuador, 113–136 mm SL, holotype and paratype*.

Silurus herzbergii **Bloch, 1794** - 9, GCRL 9591–1, Trinidad, 58–193 mm SL*. **(= type species of *Selenaspis* Bleeker).**

Arius hypophthalmus **Steindachner, 1877** - 2, USNM 76827, Panama, 195–197 mm SL*; 2, USNM 293275, Panama, 168–184 mm SL*; 2, CAS SU 7020, Panama, 188 -200 mm SL; 12, LACMNH W58-32, Mexico, 210–262 mm SL*. **(= type species of *Cathorops* Jordan and Gilbert).**

Arius insidiator **Kailola, 2000** - 4 specimens examined (Kailola 2000), all types (NTM S.11189-001, 350 mm SL, holotype; AMS I.28960-001, 282 mm SL, paratype; KFRS FO3302/AMS I.30111.001, 188 mm SL, paratype; KFRS F.5526-01, 270 mm SL, paratype)* from the Fly River to Gulf of Papua in New Guinea and east of Darwin in the Northern Territory.

Potamarius izabelensis **Hubbs and Miller, 1960** - 1, USNM 134348, Lake Ysabel, Guatemala, 213 mm SL, paratype; 2, UMMZ 177252, Lake Ysabel, 45 -51 mm SL (mouth juveniles).

Pimelodus jatius **Hamilton, 1822** - 1, AMS B.7997, Burma, Day's Collection, 159 mm SL*; 3, AMNH 17805, Monywa, Chindwin River, Burma, 144–149 mm SL*.

Arius jella **Day, 1877** - 1, ANSP 74831 (part), 72 mm SL; 1, ANSP 77252, Rangoon, Burma, 109 mm SL.

Arius kanganamanensis **Herre, 1935** - 1, CAS (SU)24450, Kanganaman, New Guinea, 176 mm SL, paratype*.

Arius kessleri **Steindachner, 1877** - 16, LACMNH unregistered, Panama, 54–412 mm SL; 1, USNM 214861, Mexico (skeleton)*; 1, USNM 214862, Pacific coast of Colombia, 135 mm SL (skeleton)*.

Bagrus laevigatus **Valenciennes, 1840** - 1, MNHN B.710, Mer Rouge, 129mm SL, type*.

Arius latirostris **Macleay, 1884** - 91 specimens examined (Kailola 1990) including syntypes (AMS I.9072, 450 mm SL; AMS I.9073, 440 mm SL; AMS I.9074, 435 mm SL; AMS I.9127, 138 mm SL)* from localities from the Vogelkopf Peninsular to Lakekamu River, southern New Guinea.

Arius layardi **Günther, 1866** - 3, LACMNH 38132-63 (in part), mouth of Turshian Creek, Sind, Pakistan, 118–128 mm SL*; 1, LACMNH 38126-20, Karachi fish market, Sind, Pakistan, 172 mm SL*; 7, LACMNH 38136-60, south of Hajambro Creek mouth, Sind, Pakistan, 149–185 mm SL*.

Arius leiotetocephalus **Bleeker, 1846** - 1, NMV 45964, East Indies Archipelago, 255 mm SL, syntype*.

Hexanematichthys leptaspis **Bleeker, 1862** - 174 specimens examined (Kailola 1990) including the holotype (RMNH 3060, 204 mm SL)* from localities from Aru Islands, Lorentz River to Vailala River, southern New Guinea and Wyndham to Archer River, northern Australia.

Arius leptonotacanthus **Bleeker, 1849** - 1, BMNH 1863.12.4:114, Madura, Indonesia, 195 mm SL, holotype*; 1, QM I.25782, Tanjung Priok, Jakarta, 245 mm SL*; 2, AMS I.41722-001, Paknam fish market, Samutprakan, Thailand, 174–188 mm SL*; 1, MCZ 23707, Penang, Malaya, 169 mm SL.

Tachysurus liropus **Bristol in Gilbert, 1897** - 3, CAS SU324, Mexico, 156–190 mm SL, paratypes*.

Arius luniscutis **Valenciennes, 1840** - 4, MCZ 7643, Bahia, Brazil, 162–192 mm SL*; 1, MCZ 7682, Cannavienias, Brazil, 212 mm SL*; 1, MCZ no number (skeleton)*; 1, AMS I.2624, Brazil, 191 mm SL*. **(= type species of *Aspistor* Jordan and Evermann).**

Arius macrocephalus **Bleeker, 1846** - 1*, BMNH 1863.12.4:78, Batavia, 308 mm SL, cotype*.

Arius macronotacanthus **Bleeker, 1846** - 1, BMNH 1863.12.4:59, Batavia, Java, 180 mm SL, syntype*; 1, RMNH 6901, Batavia fish market, Java, 232 mm SL, syntype*; 1, MZB NIP434, Pontianak, Borneo, LON stn 5 (00°05'N, 111°00'E), 106 mm SL*; 3, CAS SU 32707, Pinang, Malaysia, 148–240 mm SL; 4, UMMZ 214626, MRT#61, Truong Binh, Vietnam, 80–84 mm SL; 8, UMMZ 214629, V#66, Truong Binh, Vietnam, 49–69 mm SL; 5, LACMNH 38135-36, Hajambro Creek, Sind, Pakistan, 150–275 mm SL*.

Hemipimelodus macrorhynchus **Weber, 1913** - 13 specimens examined (Kailola 1990) from localities between the Digoel River and Purari River, southern New Guinea.

Silurus maculatus **Thunberg, 1792** - 1, MZB 2102, Belukang, Lampung Selatan, 135 mm SL*; 1, MZB NIP478, Kupang, Timor, LON stn 6, 232 mm SL*; 1, MZB NIP435, Pontianak, Borneo, LON stn 7, 107 mm SL*; 1, AMNH 9517, Borneo, 106 mm SL*; 1, AMS B.7924, Java, Day's Collection, 221 mm SL; 1, NMV 45948, East Indies Collection, Bleeker Collection A, 159 mm SL; 1, UMMZ 214646, V74-2A, Vietnam, 45 mm SL; 1, ANSP 61573-77 (part), Paknam, Thailand, 94 mm SL; 1, MCZ 30904, Jakarta, Indonesia, 78 mm SL*; 2, ANSP 60717, Bangkok, Thailand, 118–130 mm SL; 1, ANSP 60718 mm SL, 119 mm SL; 1. ANSP 60735-36 (part), Paknam, 90 mm SL; 4, ANSP 106800, Baram, Borneo, 41–190 mm SL*; 2, ANSP 61568-72 (part), Bangkok, Thailand, 40–41 mm SL; 1, LACMNH 38126-21, SL not recorded*.

Arius madagascariensis **Vaillant, 1894** - 1, MNHN 1960-236, Règion de l'Est, freshwater?, Madagascar, 140 mm SL*; 1, MNHN 1922-168, Ambatomainty, province de Maevetanana (Rivière Mahavavy), Madagascar, 61 mm SL*; 1, AMNH 17454, Madagascar, 192 mm SL*.

Arius magatensis **Herre, 1926** - 1, CAS SU29983, Cagayan Province at Aparri, Philippines, 129 mm SL*; 2, SU 13650, data not recorded, 260–350 mm SL.

Arius manillensis **Valenciennes, 1840** - 17, ANSP 98261, Manila, Philippines, 83–247 mm SL*; 1, ANSP 79490, Orion, Luzon, Philippines, 136 mm SL; 2, ANSP 79565, San Fernando, Luzon, Philippines, 187–192 mm SL; 1, ANSP 77368, Philippines, SL not recorded; 8, ANSP 49274-81, Philippines, 102–193 mm SL; 1. ANSP 123297, Manila Bay, Philippines, 246 mm SL; 6 lots, USNM, 'Albatross' material, 239–374 mm SL; 1, CAS SU35083, Manila, SL not recorded (skeleton)*; 13, ANSP 77367, Philippines, 97–114 mm SL*; 1, ANSP 98259, Laguna de Bay, Philippines, 221 mm SL.

Silurus marinus **Mitchill, 1815** - 2, AMS I.29294-001, Ship Island, Biloxi, Mississippi, 79–122 mm SL*; 1, UMMZ 200576, Guatemala, 365 mm SL (skeleton)*; 3, AMS I.37416-001, Horn Island, Mississippi, 73–102 mm SL; 1, LACMNH 32599-3, no data, 305 mm SL (skeleton)*. **(= type species of *Ailurichthys* Baird and Girard).**

Arius mastersi **Ogilby, 1898** - 25 specimens examined (Kailola 1990) including the holotype (AMS I.25690-001, 243 mm SL)* from localities between Merauke and Galley Reach in southern New Guinea and Derby and Cape York in northern Australia. Twelve paratypes of *Tachysurus (Pararius) berneyi* (AMS I.8077-I.8088, 79–116 mm SL) are also specimens of *Arius mastersi*.

Netuma mazatlana **Gilbert, 1904** - 1, CAS SU7138, Mazatlan, Sinaloa, Mexico, 227 mm SL, holotype*.

Arius melanochir **Bleeker, 1852** - 1, BMNH 1863.12.4:68, no data, 152 mm SL, type*; 2, CAS 49426 (in part), Sintang market, Kapuas, Borneo, 166–189 mm SL*; 3, USNM 230311, same data, 178–246 mm SL*. **(= type species of *Cephalocassis* Bleeker)**

Arius microcephalus **Bleeker, 1855** - 1, BMNH 1863.12.11:149, no data, 108 mm SL, syntype*; 2, unregistered, Can Tho market, Vietnam, 148–161 mm SL*; 2, UMMZ V74-36, Mekong River channel, Vietnam, 100–118 mm SL*.

Arius microstomus **Nichols, 1940** - 1, AMNH 20929, Bernhard Camp, Idenberg River, New Guinea, 74 mm SL, paratype*.

Arius midgleyi **Kailola and Pierce, 1988** - 82 specimens examined (Kailola 199) including types (AMS I.20858-006, 270 mm SL, holotype; AMNH 57454, 99 mm SL, paratype; AMNH 57454SW (in part), 106 mm SL, paratype; NTM S.11800-001, 325 mm SL, paratype; WAM P.25597-001, 348 mm SL, paratype; WAM P.25708-001, 224 mm SL, paratype; ZMA 119.467, 244 mm SL, paratype; WAM P.28776-001, 167 mm SL, paratype; WAM P.21338-002, 4 specimens, 133–161 mm SL, paratypes)* from localities between the Fitzroy River and South Alligator River, northern Australia.

Silurus militaris **Linnaeus, 1758** - 1, MZB NIP503, Tanjung Sentani, LON stn 3, 121 mm SL*; 1, LACMNH 38131-46, from

20 kilometres south of Paitiani Creek, Sind, Pakistan, 240 mm SL*; 1, LACMNH 38134-50, off Hajambro Creek mouth, Sind, Pakistan, 205 mm SL*; 1, LACMNH 38135-33, lower 10 kilometres of Hajambro Creek, Sind, Pakistan, 157 mm SL*; 1, AMS I.29295-001, Pabean, Surabaya, 1980, 285 mm SL*; 1, NMV 45847, East Indies Collection, Bleeker Collection A, SL not recorded; 1, NMV 46593, East Indies Collection, Bleeker Collection A, SL not recorded; 1, NMV 46594, East Indies Collection, Bleeker Collection A, SL not recorded; 1, UMMZ V74-42, Vietnam, 92 mm SL; 14, UMMZ V#66, Truong Binh, Vietnam, 44–149 mm SL; 1, UMMZ V#62, Truong Binh, Vietnam, 157 mm SL; 1, ANSP 74828, off Bombay, 142 mm SL; 1, ANSP 77140, same data, 127 mm SL. **(= type species of *Osteogeneiosus* Bleeker)**

***Ageneiosus mino* Hamilton, 1822** - 1, LACMNH 38116-35, Karachi fish market, Sind, Pakistan, 245 mm SL*; 1, LACMNH 38132-62, mouth of Turshian Creek, Sind, Pakistan, 225 mm SL*; 1, NMV 46019, East Indies Archipelago, Bleeker Collection A, SL not recorded. **(= type species of *Batrachocephalus* Bleeker, based on *ageneiosus* Bleeker, a junior synonym of *mino* Hamilton).**

***Arius nasutus* Valenciennes, 1840** - 1, MNHN A.9407, Malabar, 740 mm SL, syntype*; 1, MNHN A.9408, same data, 650 mm SL, syntype*.

***Pimelodus nella* Valenciennes, 1840** - 46 specimens examined (Kailola 1990) from localities between Vietnam and the Gulf of Papua, southern New Guinea and northern (Melville Island) to north-eastern (Cleveland Bay) Australia.

***Conorhynchos nelsoni* Evermann and Goldsborough, 1902** - 1, USNM 50001, Rio Usumacineta, Yucatan, 327 mm SL, type*; 1, UMMZ 198713, Rio de la Pasion, Guatemala, 480 mm SL (skeleton)*; 1, UMMZ 143498, Yalac Lake, Guatemala, 195 mm SL*; 1, UMMZ 143497, lower Rio Chajchini, Guatemala, SL not recorded; 1, UMMZ 19872, no data (skeleton)*; 1, UMMZ 28079, no data (skeleton). **(= type species of *Potamarius* Hubbs and Miller).**

***Pimelodus nenga* Hamilton, 1822** - 5, LACMNH 38132-64, Pakistan, 99–120 mm SL.

***Bagrus netuma* Valenciennes, 1840** - 1, MNHN A.9345, Pondicherry, 400 mm SL, holotype.

***Doiichthys novaeguineae* Weber, 1913** - 7 specimens examined (Kailola 1990) including syntypes (ZMA 104.122 (in part), 85–103 mm SL)* from localities between the Varen River and Purari River delta, southern New Guinea. **(= type species of *Doiichthys* Weber)**

***Arius (Brustiarius) nox* Herre, 1935** - 52 specimens examined (Kailola 1990) including 11 paratypes (FMNH 17196, 176 mm SL; FMNH 17197, 174 mm SL; FMNH 17198, 208 mm SL; FMNH 17199, 163 mm SL; FMNH 17200, 149 mm SL; CAS(SU) 24452, 3 specimens, 163–171 mm SL; CAS(SU) 24451, 2 specimens, 162–208 mm SL; CAS(SU) 69115, 153 mm SL)* from the Sepik and Ramu river systems of northern New Guinea. **(= type species of *Brustiarius* Herre).**

***Arius nudidens* Weber, 1913** - 1, MZB 129, Lorentz River, New Guinea, 67 mm SL, syntype*; 1, ZMA 111.507, Lorentz River, New Guinea, 183 mm SL, syntype*.

***Arius oetik* Bleeker, 1846** - 1, NMV 45987, East Indian Archipelago, Bleeker Collection A, 146 mm SL*; 1, MZB 1465, Sunda Strait, Palimbang, 125 mm SL*; 4, AMS I.28767-001, Songkhla market, probably from Songkhla Lake (brackish water), Thailand, 107–134 mm SL*; 16, AMS I.37421-001, same data, 109–163 mm SL; 1, AMS I.27635-002, Malaysia, 160 mm SL.

***Hemipimelodus papillifer* Herre, 1935** - 1, FMNH 17212, 224 mm SL, paratype*; 1, CAS (SU)24453, 223 mm SL, paratype*, both from Marienberg, Sepik River, northern New Guinea.

***Aelurichthys panamensis* Gill, 1863** - 1, UMMZ 177343-S, 250 mm SL (skeleton)*; 10, LACMNH W55-140, Baja, Mexico, 115-220 mm SL; 1, GCRL V79:16523, Jiquilisco Bay, El Salvador, 102 mm SL; 1, GCRL V79:16519, same data, 100 mm SL; 1, USNM 214852, Colombia, 80 mm SL (skeleton)*; 1, GCRL V79: 16675, Jiquilisco Bay, El Salvador, 139 mm SL*; 1, LACMNH 33806-128, Costa Rica, Puntarenas, 186 mm SL (skeleton)*; 1, LACMNH 33806-127, Costa Rica, Puntarenas, 196 mm SL*. **(= type species of *Anemanotus* Fowler)**

***Silurus parkeri* Traill, 1832** - 1, USNM 273376, no data (skeleton)*; 1, USNM 215204, Brazil, SL not recorded.

***Arius parvipinnis* Day, 1877** - 1, ANSP 74831 (part), Bombay, 124 mm SL*.

***Arius paucus* Kailola, 2000** - 20 specimens examined (Kailola 2000) including types (QM I.12910, 326 mm SL, holotype; QM I.12757, 310 mm SL, paratype; QM I.16730, 2 specimens, 315–329 mm SL, paratypes; QM I.11364, 205 mm SL, paratype; AMS I.25315-001, 171 mm SL, paratype; QM I.11990, 146 mm SL, paratype; QM I.16735, 240 mm SL, paratype; QM I.16738, 2 specimens, 327 mm SL and 152 mm HL, paratypes; NTM S.12070-001, 2 specimens, 298–315 mm SL, paratypes; QM I.16737, 310 mm SL, paratype; NTM S.12083-001, 331 mm SL, paratype; CAM F.35, 257 mm SL, paratype; CAM F.36, 273 mm SL, paratype) from localities between the Roper River system and Cape York, northern Australia.

***Arius pectoralis* Kailola, 2000** - 28 specimens examined (Kailola 1990) including types (AMS I.27415-001, 226 mm SL, holotype; NTM S.13004-001, 127 mm SL, paratype; CSIRO A.3608, 112 mm SL, paratype; CSIRO A.3609, 117 mm SL, paratype; CSIRO A.3610, 116 mm SL, paratype; QM I.14917, 105 mm SL, paratype; NTM S.10254-001, 2 specimens, 95–101 mm SL, paratypes; NTM S.10319-003, 56 mm SL, paratype; NTM S.10235-001, 90 mm SL, paratype; NTM S.11507-004, 145 mm SL, paratype; CSIRO H.5174-07, 4 specimens, 165–180 mm SL, paratypes; CSIRO H.4937-02, 220 mm SL, paratype) from localities ranging from the Kamora River to Kempwelch River in southern New Guinea and Darwin to the Chapman River in northern Australia.

***Pimelodus peronii* Valenciennes, 1840** - 1, MNHN 1207, 'Terres australis', 113 mm SL, holotype*.

***Galeichthys peruvianus* Lütken, 1874** - 1, AMNH 7939, Peru, 208 mm SL*; 1, USNM 36929, Callao Bay, Peru(?), SL not recorded.

***Pseudarius philippinus* Sauvage, 1880** - 1, MNHN A.2615, Lake Laglaize, Luzon, Philippines, 103 mm SL, type*.

***Arius pidada* Bleeker, 1846** - 1, BMNH 1863.12.4:57, East Indies, 190 mm SL, syntype*; 5, RMNH 6900, East Indies, 117–232 mm SL, syntypes*; 1, AMS B.7965, Java, Day's Collection, 152 mm SL, syntype*.

***Arius planiceps* Steindachner, 1877** - 1, USNM 264834, Pacific Colombia, 80 mm HL (skeleton)*.

***Netuma planifrons* Higuchi, Reis and Araujo, 1982** - 5, MCZ 58691, Rio do Sul, Brazil, 65–138 mm SL, paratypes; 1, MCZ 58691, Lagoa dos Patos, Rio Grande, Brazil, 138 mm SL, paratype*.

***Arius platypogon* Günther, 1864** - 7, LACMNH W52-252, Mexico, 196–359 mm SL; 1, USNM 214882, Colombia, SL not recorded*; 1, GCRL V84:21668, Panama, 132 mm SL*; 1, GCRL V67:2217, Panama Pacific coast, 218 mm SL*.

Arius polystaphylodon **Bleeker, 1846** - 28 specimens examined (Kailola 1990) including a syntype (BMNH 1863.12.4:98, 123mm SL)* from localities from Borneo (Sabah), Java, Bali and Humboldt Bay to the Ramu River in northern New Guinea.

Bagrus proops **Valenciennes, 1840** - 1, USNM 264836, north-eastern South America, SL not recorded (skeleton)*; 1, USNM 214860, same data?, SL not recorded (skeleton)*; 1, CAS 64043, no data (skeleton), 400 mm SL*.

Arius proximus **Ogilby, 1898** - 61 specimens examined (Kailola 1990) including the holotype (AMS I.25691-001, 338 mm SL)* from localities from the Aru Islands, Gulf of Papua to Lakekamu River (southern New Guinea) to Withnell Bay and Newcastle (Australia). **(= type species of *Pararius* Whitley, 1940).**

Arius quadriscutis **Valenciennes, 1840** - 1, USNM 215201, Brazil, 115 mm HL (skeleton)*; 1, MCZ 30097, Georgetown, Guyana, 310 mm SL*; 1, LACMNH 42611-25, Manaos, Brazil, 279 mm SL*.

Arius robertsi **Kailola, 1990** - 7 specimens examined (Kailola 1990a) including types (AMS I.27087-001, 353 mm SL, holotype; USNM 217077, 325 mm SL, paratype; KFRS F.4682-01, 350 mm SL, paratype)* from localities between the upper Fly River and the upper Purari River, southern New Guinea.

Arius rugispinis **Valenciennes, 1840** - 1, MCZ 30101, Georgetown, Guyana, 235 mm SL*; 2, MCZ 7720, Para, Brazil, 186–224 mm SL*.

Pimelodus sagor **Hamilton, 1822** - 5, AMS I.41724-001, Songkhla market, caught in Songkhla Lake, Thailand, 185–198 mm SL*; 1, ZMB 31875, same data, 183 mm SL*; 3, CAS SU 27734, Sandakan, north Borneo, 143–233 mm SL*; 3, MZB NIP3831, Muarakarang, Jakarta, LON stn 8, 64–68 mm SL; 5, MZB 1470, Gulf of Banten, west Java, 55–120 mm SL*; 1, MZB NIP3830, Muarakarang, Jakarta, LON stn 4, 86 mm SL*; 1, AMNH 9293, Sumatra, 92 mm SL*; 7, CAS SU 29454, Sandakan, north Borneo, 48–52 mm SL*; 3, CAS SU32709, Tawau, north Borneo, 180–212 mm SL*; 1, ANSP 91825, Borneo, 250 mm SL; 1, ANSP 91824, Borneo, 241 mm SL; 1, ANSP 136677, Borneo, 120 mm SL; 1, ANSP 91823, Borneo, 250 mm SL; 1, ANSP 86187, Singapore, 220 mm SL; 1, UMMZ 155782, Java, 1929, SL not recorded; 1, UMMZ 55783, Java, SL not recorded; 1, AMS B.8017, Moulmein, Burma, Day's Collection, 200 mm SL; 1, NMV 46559, East Indies Archipelago, Bleeker Collection A, SL not recorded; 1, MCZ 7714 (part), Penang, Malaysia, 141 mm SL; AMS IA.3226, Malaysia, 69 mm SL. **(= type species of *Hexanematichthys* Bleeker, based on *sondaicus* Valenciennes, a junior synonym of *sagor* Hamilton).**

Arius sagoroides **Hardenberg, 1941** - 1, NCIP 516, Octokwa River mouth, southern New Guinea, 242 mm SL, probable syntype* (Kailola 1990).

Arius satparanus **Chaudhuri, 1916** - 2, LACMNH 38136-59, Hajambro Creek, Pakistan, 130–168 mm SL; 6, LACMNH 38131-47, same data, 108–146 mm SL; 2, LACMNH 38134-31, same data, 115–126 mm SL; 4, LACMNH 38133-69, same data, 108–128 mm SL; 3, LACMNH 38314-46, Baluchistan, Sonmiani Bay, 215–240 mm SL; 3, LACMNH 38313-53, same data, 208–238 mm SL; 13, LACMNH 38130-80, Sind, Pakistan, 106–185 mm SL.

Arius schlegeli **Bleeker, 1863** - 1, AMS B.8123, Amoy, China, 178 mm SL, cotype*; 3, RMNH 3032 (in part), Amoy, China, 142–237 mm SL (material identified by Bleeker (1863) as conspecific).

Arius sciurus **Smith, 1931** - 1, USNM 90310, Tapi River, Thailand, 202 mm SL, holotype*.

Arius seemanni **Günther, 1864** - 8, GCRL V70:5113, 03°49'N, 77°11'W, Colombia, 88–119 mm SL*; 1, USNM 79377, no data, SL not recorded.

Arius serratus **Day, 1877** - 1*, AMS B.7971, Sind, 128 mm SL*.

Arius (Brustiarius) solidus **Herre, 1935** - 150 specimens examined (Kailola 1990) including 17 paratypes (FMNH 17202, 189 mm SL; FMNH 17203, 175 mm SL; FMNH 17204, 154 mm SL; FMNH 17205, 150 mm SL; FMNH 17206, 185 mm SL; FMNH 17207, 197 mm SL; FMNH 17208, 185 mm SL; CAS(SU) 24445, 4 specimens, 135–191 mm SL; CAS(SU) 24444, 5 specimens, 140–234 mm SL; CAS(SU) 24447, 224 mm SL)* from Mamberamo, Idenberg, Sepik and Ramu river systems of New Guinea.

Pimelodus sona **Hamilton, 1822** - 1, AMS B.7953, Calcutta, India, Day's Collection, 280 mm SL*; 2, LACMNH 38130-81, 20 kilometres south of Paitiani Creek, Sind, Pakistan, 188–234 mm SL*; 1, LACMNH 38133-71, 3–4 kilometres west of Turshian Creek mouth, Sind, Pakistan, 162 mm SL*; 1, AMS IA.2663, Bandar, Maharani, Johor state, Malaya, tank specimen, SL not recorded; 1, MCZ 23739, Singapore?, 214 mm SL; 1, MCZ 7723 (part), Hong Kong, 215 mm SL; 3, MCZ 7714 (part), Penang, Malaysia, 185–236 mm SL; 2, USNM 149731, Travancore, India, 86–111 mm SL; 1, ANSP 77127, off Bombay, 85 mm SL; 1, ANSP 74890, off Bombay, 93 mm SL; 3, ANSP 74851, Calcutta, 44–57 mm SL.

Arius spatula **Ramsay and Ogilby, 1886** - 18 specimens examined (Kailola 1990) including the holotype (AMS B.9937, 255 mm SL)* from localities ranging between the Lorentz River and the Lakekamu River, southern New Guinea. **(= type species of *Cochlefelis* Whitley).**

Pimelodus spixii **Agassiz, 1829** - 1, MCZ 114, no data, 164 mm SL*.

Tachysurus steindachneri **Gilbert and Starks, 1904** - 1, CAS SU 7027, Panama, 205 mm SL, paratype*; 1, CAS SU 7026, Panama, 166 mm SL*; 2, AMNH 32448, Santa Rosa, Guatemala, 148–155 mm SL*.

Cephalocassis stormii **Bleeker, 1858** - 1, RMNH 6893, Sumatra?, 340 mm SL, syntype*; 1, BMNH 1863.12.4:65, Sumatra, 280 mm SL, syntype*; 1, CAS 49427, Kapuas River basin, Borneo, 393 mm SL*; 1, USNM 230312, Sintang market, Kapuas River basin, Borneo, 288 mm SL*; 1, UMMZ 214619, Mekong River channel, My Tho, Vietnam, 99 mm SL; 4, LACMNH 38131-50, Sind, Pakistan, 147–270 mm SL*; 1, UMMZ 155676, Palembang, Sumatra, 221 mm SL*; 1, ANSP 88953, Medan, Sumatra, 36 mm SL; 12, ANSP 60720-32 (part), Bangkok, Thailand, 62–73 mm SL*; 1, UMMZ 214611, Vietnam, 136 mm SL; 1, UMMZ 214609, Vietnam, 268 mm SL; 2, ANSP, data not recorded, 81–82 mm SL*. **(= type species of *Hemiarius* Bleeker).**

Arius stricticassis **Valenciennes, 1840** - 1, MCZ 7717, Maranhao (S. Luis), Brazil, 219 mm SL; 1, MCZ 7639, Bahia (Salvador), Brazil, 188 mm SL; 1, MCZ 7640, Bahia (Salvador), Brazil, 129 mm SL.

Arius subrostratus **Valenciennes, 1840** - 1, AMS B.7610, Canara, India, Day's Collection, 275 mm SL*; 1, AMS B.7611, same data, 157 mm SL; 1, MCZ 4275, Canara, India, 170 mm SL; 1, MCZ 4275, Canara, India, 170 mm SL; 1, USNM 149730, Travancore, India, 152 mm SL.

Hemipimelodus taylori **Roberts, 1978** - 7 specimens examined (Kailola 1990a) including types (AMS I.27087-001, 353 mm SL, holotype; USNM 217077, 325 mm SL, paratype; KFRS F.4682-01, 350 mm SL, paratype)* from localities between the upper Fly River and the upper Purari River, southern New Guinea.

***Arius tenuispinis* Day, 1877** - 1, MCZ 59239, Khor Al Sabiya, Kuwait, 130 mm SL; 1, UMMZ unregistered, V74 stn 9A#98, 225 mm SL (brooding male); 1, UMMZ 214637, Vietnam, 122 mm SL; 4, LACMNH 38129-93, off mouth of Korangi Creek, Sind, Pakistan, 131–160 mm SL*.

***Netuma thalassina jacksonensis* Whitley, 1941** - 1, AMS I.10095, Port Jackson, 293 mm SL, holotype*.

***Bagrus thalassinus* Rüppell, 1837** - 132 specimens examined (Kailola 1990) from localities from Ethiopia to Sydney Harbour, Australia*. **(= type species of *Netuma* Bleeker, based on *netuma* Valenciennes, a junior synonym of *thalassinus* Rüppell).**

***Arius tonggol* Bleeker, 1846** - 1, BMNH 1863.12.4.56, 'East Indies', 285 mm SL, syntype*.

***Sciades troschelii* Gill, 1863** - 4, LACMNH W58-38, Mexico, 133 mm SL*; 1, USNM 214858, Mercado, Pacific Colombia, SL not recorded; 1, USNM 214864, Pacific Colombia, 100 mm HL (skeleton)*; 1, CAS 12067, Mazatlan, Mexico, SL not recorded (skeleton)*. **(= type species of *Sciadeops* Fowler).**

***Arius truncatus* Valenciennes, 1840** - 1, MZB 2161, no data, 185 mm SL*; 3, CAS 32710, Kuala Kangsar, Perak, Malaysia, 185–224 mm SL*; 1, ANSP 61636, Sriraja, Thailand, 163 mm SL; 1, USNM 103185, Bangpakong River, Thailand, 266 mm SL*; 1, ANSP 60720-32 (part), Bangkok Thailand, 57 mm SL; 3, USNM 103183, central Siam, 150–247 mm SL; 1, UMMZ V74-57, Can Tho Island, Vietnam, 93 mm SL; 1, ANSP 59430, Bangkok, Thailand, 158 mm SL*; 1, ANSP 59468, Bangkok, Thailand, 55 mm SL; 1, ANSP 60719, Bangkok, 64 mm SL; 1, ANSP 61636, Sriraja, Thailand, 163 mm SL*; 2, AMS I.28082-041 (part), Malaysia, 182–260 mm SL; 1, AMS I.27635-001, Malaysia, 285 mm SL. **(= type species of *Cryptarius* n. gen.).**

***Ketengus typus* Bleeker, 1847** - 1, BMNH 1863.12.4:112, no data, 188 mm SL, syntype*; 2, BMNH 1855.9.19:1110-1111, no locality, Haslar Collection, 78-mm SL*; 1, ZMA 119.360, Batu Pangal, Kutei (= Mahakkan) River, Borneo, 122 mm SL*; 1, NMV 46234, East Indies Archipelago, Bleeker Collection A, SL not recorded; 5, ANSP 60704-8, Bangkok, Thailand, 35–130 mm SL*; 1, ANSP 61539, Bangkok, 89 mm SL; 1, ANSP 59466, Bangkok, 58 mm SL. **(= type species of *Ketengus* Bleeker).**

***Arius utarus* Kailola, 1990** - 103 specimens examined (Kailola 1990a) including types (AMS I.25406-001, 270 mm SL (holotype), RMNH 28814, 88 mm SL; ZMA 116.459, 250 mm SL; ZMA 116.460, 267 mm SL, RMNH 8001, 149 mm SL (syntype of *Hemipimelodus velutinus* Weber); AMS I.25406-002, 2 specimens, 242–285 mm SL; WAM P.27846-001, 4 specimens, 97–133 mm SL; WAM P.27847-010 (7); P.28224-00, 253 mm SL; QM I.21674, 294 mm SL; SAMA F.6254, 176 mm SL; CSIRO C.3532, 122 mm SL; CAS (SU) 68631, 198 mm SL; CAS (SU) 28204, 218 mm SL; CAS (SU) 68882, 198 mm SL; CAS 13482, 2 specimens, 215–280 mm SL; CAS 3481, 380 mm SL; WAM P.27847-009, 11 specimens, 84–118 mm SL; KFRS F.5517-01, 2 specimens, 297–325 mm SL; NTM S.11904-001, 2 specimens, 252–258 mm SL)* from localities between the Mamberamo River and the Ramu River, northern New Guinea.

***Hemipimelodus velutinus* Weber, 1908** - 67 specimens examined (Kailola 1990) including syntypes (ZMA 112.656 (in part), 133–148 mm SL)* from localities between the Mamberamo River and the Ramu River, northern New Guinea.

***Arius venosus* Valenciennes, 1840** - 1, MNHN 1205 (in part), Rangoon, Burma, 230 mm SL, syntype*; 1, MZB 098, Batavia, Java, 185 mm SL*; 1, ANSP 90521, Bombay, India, 280 mm SL; 4, CAS SU 27749, Sandakan, Borneo, 140–172 mm SL; 1, MCZ 7714 (part), Penang, Malaysia, 170 mm SL*; 1, MCZ, 4384, Bangkok, 240 mm SL; 1, AMS I.28986-010, Malaysia, 155 mm SL.

***Galeichthys xenauchen* Gilbert in Jordan and Evermann, 1898** - 1, CAS SU5821, Panama, 314 mm SL, type*.

***Arius* species** - 6, AMS I.41721-001, Paknam market, Samutprakan, Thailand, 129–210 mm SL*; 1, LACMNH 38128-47, Hawkes Bay, west of Karachi, Sind, Pakistan, 194 mm SL*; 1, MCZ 27053 (part), Singapore, 237 mm SL*; 1, USNM 52670, no data, 290 mm SL; 2, MCZ 7714 (part), Penang, Malaysia, 208–215 mm SL; 1, ANSP 51335, Ceylon, Colombia, 1924, 34 mm SL.

***Cathorops* spp** - 17, USNM 286395, off Surinam, 62–102 mm SL; 5 lots, USNM 214866-214872, Colombia to Brazil (skeletons)*; 1, LACMNH 33806-93, Costa Rica, 266 mm SL (skeleton)*; 5, GCRL V81:17226 (part), Surinam, 112–237 mm SL*; 3, GCRL V79:16676, Jiquilisco Bay, El Salvador, 121–142 mm SL.

APPENDIX B. Outgroup taxa examined.

Bagridae – *Bagrichthys macropterus*, 1, dry skeleton, UMMZ 201686-S, Thailand, 227 mm SL; *Bagrus docmak*, 1, dry skeleton, UMMZ 187332-S, Paraguay, SL not recorded; *Chrysichthys auratus*, 1, dry skeleton, UMMZ 210275-S, Egypt, 176 mm SL; *Mystus* species, 1, unregistered, Surabaya, Java, 130 mm SL; *Rita chrysea*, 6, ex CAS 54540, Orissa Province, India; *Rita kuturnee*, 2, CAS 48798, Andrha Pradesh, India, SL not recorded, 2, CAS 34868, Maharastra Province, India, SL not recorded; *Rita* species, 1, CAS SU41044, Andrha Pradesh, India, SL not recorded; *Rita rita*, 11, CAS 34866, Hugli River, India.

Callichthyidae – *Brochis splendens*, 1; *Dianema longibarbis*, 1; *Dianema urostriatum*, 1. All bought from pet fish stores; SLs not recorded.

Diplomystidae – *Diplomystes chilensis*, 1, CAS 45718, Chile; 1, CAS SU23963, Chile. SLs not recorded.

Doradidae – *Anadoras grypus*, 1, ex USNM 284601, Brazil, 80mm SL; *Pterodoras* species, 1, ex USNM 257988, Venezuela, 82 mm SL.

Heptapteridae – *Rhamdia laticauda*, 1, ex USNM 114359, Guatemala, 101 mm SL; *Rhamdia quelen*, 1, dry skeleton, UMMZ 207348-S, Paraguay, SL not recorded.

Ictaluridae – *Ictalurus punctatus*, 1, dry skeleton, UMMZ 169030-S, Missouri, 265 mm SL; *Noturus flavus*, 1, dry skeleton, UMMZ 189178-S, Michigan, 232 mm SL; 1, dry skeleton, UMMZ 194599-S, Michigan, 148 mm SL; *Pylodictus olivaris*, 1, dry skeleton, UMMZ 169029-S, Missouri, 434 mm SL.

Loricariidae – *Hypostomus plecostomus*: information from Schaefer (1987).

Mochokidae – *Synodontis macrostigma*, 1, dry skeleton, UMMZ 200089-S, Kafue River, Zambia, 125 mm SL.

Pangasiidae – *Pangasius hypophthalmus*, 1. Bought from a pet fish store; SL not recorded.

Pimelodidae – *Pimelodus blochii*, 1, ex USNM 258185, Venezuela, 79 mm SL.

Plotosidae – *Neosilurus* species, 2, unregistered, Kimberley area, NW Australia, 81 and 93 mm SL.

Schilbeidae – *Schilbe mystus*, 1, dry skeleton, UMMZ 200154-S, Kafue River, Zambia, 170 mm SL.

Siluridae – *Ompok leiacanthus*, 1, SL not recorded; *Ompok miostoma*, 1, SL not recorded; *Parasilurus asotus*, 1, dry skeleton, UMMZ 187595-S, Lake Biwa, Japan, 145 mm SL; *Silurichthys phaiosoma*, 1, SL not recorded (unregistered material bought from pet fish stores).

TAXONOMIC INDEX

Bold and italic numerals indicate respectively species illustrations and the formal description of genera.